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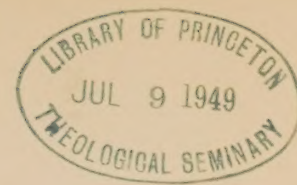




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# AMERICAN MESOZOIC MAMMALIA

BY

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## PREFACE

WORK on this memoir was begun in October, 1924, and by September, 1926, the actual examination and description of material was complete. The following year was spent in Europe studying Mesozoic mammals as a National Research Fellow in the Biological Sciences and the chief results have been published in a memoir (Simpson, 1928B) which includes all known European Mesozoic mammals and a few others. In the light of this thorough review of the related European forms, the present memoir was entirely revised and rewritten, bringing it into the form in which it now appears. Although each is a distinct unit, the American and European memoirs are complementary. Repetition has been reduced to a minimum, and for a view of the whole subject both should be consulted.

A number of papers have been published in the *American Journal of Science* under the general title of "Mesozoic Mammalia" (1925-28). Several of these papers are not merely preliminary as regards the subject of the present work but are also supplementary. It has not been thought necessary to repeat here all the morphological details of, for instance, the American Triconodonta and Symmetrodonta, although for the sake of completeness the various genera and species are redefined and some additions and corrections due to subsequent work are made.

Of the three known African Mesozoic mammals, *Tritylodon* finds a place in the European Memoir, *Archaeodon* in "Mesozoic Mammalia. X," and *Brancatherulum* in "Mesozoic Mammalia. XI." The one known South American mammal of probable Mesozoic age is considered in the present work. The known Mongolian Mesozoic mammals have been treated in one paper by Gregory and Simpson and three by Simpson in the *Novitates* of the American Museum of Natural History. This publication thus marks the completion of a series of studies which includes all the Mesozoic mammals now known.

This memoir is based primarily on the magnificent Marsh Collection in the Peabody Museum of Yale University, the largest collection of Mesozoic mammals in the world, and except for the final revision and rewriting the work has been carried out in the Peabody Museum.

In its original form, this memoir was presented in 1926 as a Dissertation to the Faculty of the Graduate School of Yale University, in Candidacy for the Degree of Doctor of Philosophy.

The writer is deeply indebted to Professor R. S. Lull who made this undertaking possible and who has constantly facilitated its conclusion. The trustees of the Othniel Charles Marsh Publication Fund generously provided a fellowship for this purpose for two years and also provided for the illustration of the Peabody Museum material and for various incidental expenses. Dr. J. W. Gidley allowed free access to the very

important material in his care and permitted its inclusion in this study—an action the more liberal and disinterested in that he had himself performed the laborious task of preparing these specimens for study and had planned eventually to monograph them. The authorities of the United States National Museum also provided numerous photographs for study and publication. Mr. O. A. Peterson brought to New York for the author's study the whole of the Lance mammal collection in the Carnegie Museum. Professor W. J. Sinclair permitted examination of the Lance mammals in the Geological Museum of Princeton University. The rich Mesozoic mammal collections of the American Museum of Natural History were placed freely in the author's hands, both before and since his official connection with that institution. Professor Henry Fairfield Osborn, Dr. W. D. Matthew, and Dr. W. K. Gregory have all taken a constant and helpful interest in the work. Many other friends and colleagues have placed the author in their debt in ways more difficult of formal acknowledgment.

Unless otherwise credited, the drawings were made by Rudolph Weber and Mrs. Louise Nash and the photographs by the author.

The manuscript was complete in its present form on May 1, 1928, but in some cases it has been possible to take cognizance of work published since that date.

G. G. S.

*New York,*

*December 13, 1928.*



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# AMERICAN MESOZOIC MAMMALIA

## I. INTRODUCTION

THE known specimens of Mesozoic mammals are among the most precious and important remains of extinct life which have yet been discovered. They are the sole direct evidence of the fundamental first two-thirds of the evolution of the Class Mammalia, which is now dominant on the earth and to which we ourselves belong. This importance has long been rather vaguely recognized, but it can hardly be said to have been properly evaluated. The Mesozoic forms are usually briefly dismissed as being rare, fragmentary, and poorly understood—accusations which are true, but not in the accepted degree. The Mesozoic mammals are now represented by many hundreds of specimens derived from all the continents save Australia and coming from various horizons from the close of the Triassic to the first appearance of abundant mammals in the lowest Paleocene.

The larger part of this material is from Europe and North America. That from North America is almost all in the Marsh Collection, now divided between the Peabody Museum of Natural History of Yale University and the United States National Museum. Smaller, but still very important, collections are preserved in the American Museum of Natural History and some other institutions have a few specimens. Especially as regards the earlier and more important Morrison fauna, this material is of unexpected richness. Professor O. C. Marsh studied his great collection only in a very preliminary and cursory way. He planned to return to it and to monograph it thoroughly, but that plan was destined never to be fulfilled. The study of this material has thus remained an outstanding necessity. That a restudy and revision of Marsh's types, in the light of the advances of so many years, were necessary has long been evident, but it was not suspected that a large part of the collections had never been studied or that they contained so much that is entirely new.

It is now well over one hundred years since Buckland announced the discovery of Mesozoic mammals (1824). The lively discussion that followed that announcement and ended in establishing beyond question the presence of mammals in the Secondary was based altogether on English material, chiefly from Stonesfield (middle Jurassic). Further discoveries in the Stonesfield "slate," in the late Jurassic Purbeck beds, and in the earlier Rhaetic beds followed, until by 1871, the date of Sir Richard Owen's monumental memoir on the fossil mammals of the Mesozoic, almost as many European specimens were known as at the present time. The discovery and description of the equally important and somewhat more abundant American forms, on the contrary, has been wholly subsequent to that date. The year 1871 thus forms a convenient and natural dividing line between two very distinct phases of the history of the subject.<sup>1</sup>

<sup>1</sup> The history of the discovery of the European specimens is more fully given in the writer's *Catalogue of Mesozoic Mammalia in the . . . British Museum* (1928).

The first reputed American Mesozoic mammal was *Dromatherium*, described by Emmons in 1857. Although this form and a second genus, *Microconodon*, described by Osborn, were for many years widely accepted as mammals, this status was several times challenged and in a recent exhaustive study (1926E) the present writer has attempted to show that both genera should be referred to the Reptilia and that true mammals are as yet unknown in the American Triassic. It was not until the epoch of the first extensive explorations for dinosaurs in the American West that the first true Mesozoic mammals were found.

Although some isolated specimens of dinosaurs had previously found their way to the East, it was not until 1877 that the true discovery of our western dinosaur fields was made. In that year abundant remains were found almost simultaneously at several points in Colorado and Wyoming. One of these localities was Como Bluff in southwestern Wyoming, a locality to which the still unwritten story of early American exploration for fossils will necessarily devote one of its most fascinating chapters. One of the original discoverers soon passed from the scene, but the other, William H. Reed, was, if not continuously present, never long absent. Most of the earlier work here was done by him or under his direct guidance. Early in 1878 Reed discovered and sent to Professor Marsh in New Haven a small broken jaw with a single tooth. This was at once recognized as a Jurassic mammal and became in the same year the type of *Dryolestes priscus* Marsh. The field workers were directed to bend all their energies to the discovery of other jaws. It was in 1879 that the now famous Mammal Quarry, Quarry 9, was discovered. With the exception of the first specimen (from the surface at some distance from Quarry 9), of one from Quarry 11, also at Como Bluff, and of three from Canyon City in Colorado, all of the hundreds of mammals from the Morrison formation came from this one quarry. Although the dinosaur quarries, especially the almost equally famous Quarry 13, were often worked instead or simultaneously, work continued in Quarry 9 for several years.

The size of the collection thus made can be judged from the fact that at Yale alone there are about two hundred and fifty separate specimens of jaws or teeth from Como Bluff, mostly very fragmentary to be sure. Marsh published the most striking of this material as it came to his hand (1878, 1879A, -B, -C, 1880, 1881). In 1887 he published a regrettably brief general paper in which all the previously mentioned forms were reviewed and several new ones added, with woodcuts of at least one specimen of each genus as then understood. At this time there were noticed 14 genera with 25 species, and until 1925 no new ones were added to the list of Morrison mammals.

The year 1888 was notable for the appearance of the second comprehensive memoir on the Mesozoic Mammalia, that of Professor Henry Fairfield Osborn.<sup>2</sup> This was, until the present work, the only comprehensive study including the many forms discovered between 1871 and 1887 and it contains the first attempt to place all these animals in a natural zoölogical classification. Based chiefly on a review of the British Museum collections, it necessarily relied on the published data for the American

<sup>2</sup> The first was that of Owen in 1871.



forms, and the avowedly incomplete nature of Professor Marsh's studies made a thorough synthesis impossible. The fact that this memoir and Marsh's paper of 1887 have remained the authorities for Jurassic mammals for over forty years is a monument to their high quality. That many changes, some fundamental, are now necessary bespeaks only the inevitable advance of knowledge, the availability of materials then unstudied, and the possibility of first-hand comparisons then impossible.

Although the earlier Mesozoic mammals were thus slowly being made known, both in Europe and in America, there remained a vast gap between the close of the Jurassic and the dawn of the Tertiary in which no mammals were known. The filling of this gap has been very slow, and it remains in essence the greatest single break in our knowledge of mammalian history. A number of vitally important Cretaceous mammalian faunas have, however, since come to light.

In 1876 Cope described a single tooth from the upper Cretaceous of Montana under the name *Paronychodon*, a genus now recognized as mammalian although described as reptilian. In 1882 J. L. Wortman found in beds of similar age in South Dakota two teeth and a fragmentary humerus which Cope named *Meniscoessus conquistus*, the first recognized Cretaceous mammal. One of the teeth later proved to belong to an armored dinosaur, but this cannot be supposed to invalidate the discovery.

The whole problem of mammals in the upper Cretaceous remained rather dubious, however, until 1889 when J. B. Hatcher was in what was then Converse County<sup>8</sup> in Wyoming, collecting dinosaurs. A futile search had been made in Montana and South Dakota for mammals during the preceding year, but in the Wyoming field Hatcher was amply compensated for previous disappointments by the discovery of quantities of mammal teeth near his ceratopsian dinosaur localities. Between 1889 and 1892 were made the large collections, comprising many hundreds of isolated teeth, fragmentary jaws, and skeletal parts now preserved at Yale and in the National Museum. Hatcher was assisted by several other workers, of whom O. A. Peterson is especially worthy of mention, and in 1889-90 Professor Beecher of Yale was also in the field and made large collections. These tiny and fragmentary remains were almost all picked up on the surface where they had accumulated as the finer material was blown away by the wind. The majority of them were found in the numerous ant hills of the region, a unique occurrence of fossils—collected by insects in their underground burrows, brought to the surface with other material, sifted by the wind, and awaiting only the selective agency of man. (See Lull, 1915A, -B.) The results of these efforts were embraced in a series of three papers by Marsh (1889A, -B, 1892). Here again his work was intended only to be preliminary and a synthesis was left for a projected monograph which he did not live to complete.

In 1891 parts one and two of Marsh's three papers, collectively titled "Discovery of Cretaceous Mammalia," were critically reviewed by Osborn, who attempted the first correlation of the tooth types into natural genera. Marsh's few further publications on Mesozoic mammals were chiefly of a polemic nature and his monumental labors on this subject must be considered as virtually ending in 1892.

<sup>8</sup> This old county has since been divided and the locality in question is now in Niobrara County.



After Marsh's retirement from the field, further collecting in the Jurassic has been largely negative in results, but knowledge of Cretaceous mammals of the world has been continually increasing to the present time. In 1892 Wortman discovered a fragmentary specimen which had the peculiar virtue of showing upper and lower teeth in association. This important form Cope described as *Thlaeodon padanicus*. In the same year Wortman and Peterson made a collection for the American Museum at Marsh's Wyoming localities which was described in a paper by Osborn in 1893. In treating the early evolution of the Amblypoda in 1898 Osborn returned to some of this material and applied names to three types left nameless in the earlier work.

Save for the rather doubtful *Paronychodon*, all the American Cretaceous mammals so far known had come from the Lance and its equivalents, but in 1902 Lawrence Lambe described two new forms from the Belly River of Alberta, a horizon equivalent to the Judith River of Montana and older than the Lance. Working in the same beds in 1915, Barnum Brown discovered an unusually fine specimen, later described by W. D. Matthew (1916) as *Eodelphis browni*. Another nearly complete lower jaw from the same formation was sent to the British Museum by William E. Cutler and was named *Cimolestes cutleri* by A. Smith Woodward in a paper appearing almost simultaneously with that of Matthew.

In 1915 R. S. Lull published a detailed and valuable stratigraphic paper on the Lance mammal occurrences, but only a few small and more or less casual collections have since been made. It remains only to mention that a small but important collection had been made in 1907 in Montana beds equivalent to the Lance by Barnum Brown. This collection was not described until 1927 (Simpson, 1927A).

The importance of the Mesozoic mammals in the literature has been much enhanced by the central place which they have rightly come to occupy in the numerous theories of molar evolution, especially in the arguments of what has been called the American School. Osborn's *Evolution of Mammalian Molar Teeth* (1907) contains the essence of his deductions in this respect, and also a new classification of Mesozoic mammals which serves as a point of departure for later work. In 1906 J. W. Gidley published excellent figures of a few of the teeth in the United States National Museum and based on them a criticism of the Cope-Osborn theory.

Expressed as briefly as is consistent with proper recognition of a great debt to the past, such are the steps by which the foundation for the present more general work was laid. The scope of this memoir is adequately represented by its title—all American Mesozoic mammals are included, with the understanding that for present purposes the Lance is accepted as the last Mesozoic and the Puerco as the first Tertiary horizon. The problems here considered are threefold: morphologic, taxonomic, and geologic. The morphologic results are kept objective, as far as possible, and are documented largely by illustrations of the critical material. The taxonomic results are based on this newer and more extensive morphologic knowledge, on detailed comparisons with European material, and on the general advance in knowledge of the last years. They have a firmer basis in objective observation than has hitherto been possible, but like all previous classifications this one is obviously liable to radical revision by future work.

The data here presented are intricately bound up with broader questions, notably that of the origin of the Mammalia and that of the evolution of the mammalian dentition, but these highly theoretical and controversial topics are not here treated, save incidentally. The presentation of the actual data is conceived to be of more immediate importance than the attempted correlation of these facts with current speculations, although such a correlation is also an eventual necessity and will be undertaken at another time.

## II. MORPHOLOGY AND TAXONOMY

As already intimated, the American Mesozoic mammals fall naturally into two great faunal groups, the Jurassic mammals and those of the upper Cretaceous. Even from a strictly taxonomic viewpoint, this division is a natural one, for only one order, the Multituberculata, is common to the two groups and even it suffered a great change in

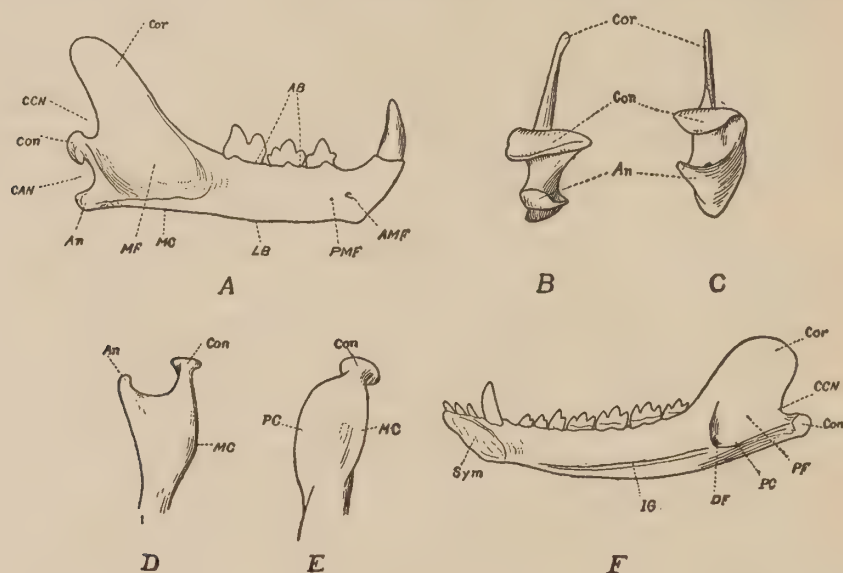


FIG. 1. Diagram to illustrate common descriptive terms applied to the mammalian mandible. A, *Felis*, external view. B, *Felis*, posterior view. C, *Bettongia*, posterior view. D, *Bettongia*, inferior view of posterior part of mandible. E, *Djadochtherium*, inferior view of posterior part of mandible. F, *Priacodon*, internal view. All right rami, not to scale.

AB, alveolar border. An, angle or angular process. CAN, condylo-angular or subcondylar notch. CCN, condylo-coronoid or supracondylar notch. Con, condyle. Cor, coronoid process. DF, dental foramen. IG, internal groove. LB, lower border. MC, masseteric crest. MF, masseteric fossa. PC, pterygoid crest. PF, pterygoid fossa. PMF, posterior mental foramen. Sym, symphysis.

the interval. Jurassic mammals are known in America only from a single formation, the Morrison, which marks the close of the period.<sup>1</sup> All of the Jurassic species known

<sup>1</sup> As is well known, the Morrison is almost exactly on the line between Jurassic and Cretaceous, often being referred to the latter period. The writer's reasons for retaining it in the Jurassic have been given elsewhere (1926F). In any event its relative position is not in question and the argument is not very important.



are, therefore, nearly or quite contemporaneous. The upper Cretaceous mammals come from two or three distinct, successive horizons, but they constitute an essential faunal unit not possible of division at present, and their treatment together is entirely justifiable whether from a zoölogical or geological point of view.

## A. MAMMALS OF THE MORRISON FORMATION, UPPER JURASSIC

THE mammalian fauna of the Morrison formation is at present by far the largest and most important of the entire Mesozoic. Although it is exceeded in the completeness of individual specimens by the South African Stormberg and the Mongolian Djadokhta, yet it leads almost incomparably in the number and variety of known forms and it is the real basis of our present knowledge of Jurassic mammals. As is brought out more fully elsewhere, it is essentially contemporaneous with the rich Purbeckian mammalian fauna of England. The families, the genera, and, where necessary, the species of the two faunas have been very closely compared.

Four orders here occur: Multituberculata, Triconodonta, Symmetrodonta, Pantotheria. In the following revision seven families, twenty-four genera, and forty species are recognized. The number of genera and species would be somewhat reduced by the discovery of associated material, but the fauna will remain comparable to many Tertiary mammalian faunas in variety.

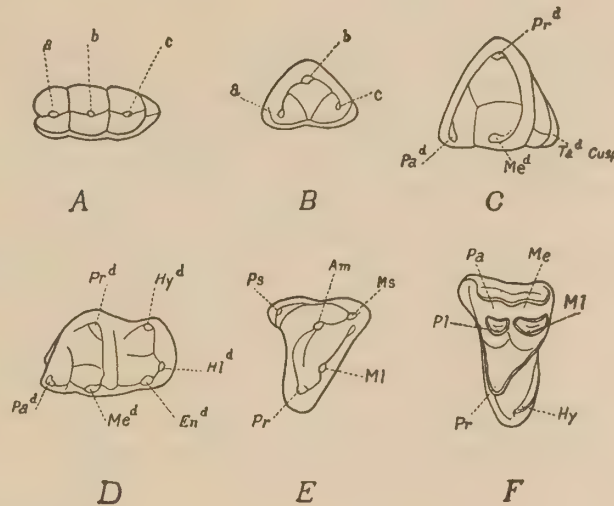


FIG. 2. Diagrams to illustrate terms applied to molar cusps and their abbreviations. A, *Priacodon*, lower molar. B, *Tinodon*, lower molar. C, *Dryolestes*, lower molar. D, Lance didelphid, lower molar. E, *Melanodon*, upper molar. F, *Gypsonictops*, upper molar.

a, b, c, the anterior, median, and posterior cusps, respectively, of triconodonts or symmetrodonts. Am, amphicone, or median external cusp of pantothere upper molars. En<sup>d</sup>, entoconid. Hl<sup>d</sup>, hypoconulid. Hy, hypocone. Hyd, hypococonid. Me, metacone. Me<sup>d</sup>, metaconid. Ml, metaconule. Mts, metastyle. Pa, paracone. Pa<sup>d</sup>, paraconid. Pl, paraconule. Pr, protocone. Pr<sup>d</sup>, protoconid. Ps, parastyle. Ta<sup>d</sup> cusp, talonid cusp of pantotheres.

## ORDER MULTITUBERCULATA Cope

DEFINITION.—Upper incisors primitively three, the first much reduced or lost, the second enlarged. One enlarged lower incisor. No canines. Molars with five or more cusps arranged in two parallel longitudinal rows in the lower jaw, in two or three

rows in the upper jaw. Nasals large, expanded posteriorly. Zygomata arising opposite middle or anterior cheek teeth, widely expanded. Post-glenoid region very short or practically absent. Mandible powerful, with small, low coronoid and no true angular process, but with a well marked pterygoid crest.

DISTRIBUTION.—Triassic, Europe, South Africa. Jurassic, Europe, North America. Cretaceous, Mongolia, England, North America. Paleocene, Mongolia, France, North America. Eocene, North America (Wyoming).

Judged by any criteria other than those of the student of Holocene zoölogy, this is one of the greatest of all mammalian orders. Although the multituberculates have apparently been totally extinct since early in the true Eocene, the recorded history of the group is longer than that of any other order of mammals. They are known from almost every Mesozoic or Paleocene mammalian horizon and, despite the present imperfection of our knowledge, it is probable that they were as truly world-wide in distribution as any mammalian order has ever been, with the exception of the primates. With few exceptions, their remains are rare and often leave much to be desired, but even our present relatively scanty record shows that they included a very wide range in morphology and in size. About twenty-five well distinguished genera are now known and even this scattering record shows differences in form and in bulk which compare favorably with many of the vastly better known Tertiary and recent orders.

The first presumable multituberculate was described by Plieninger in 1847<sup>2</sup>—“*Microlestes*” (now correctly *Thomasia*) from the Rhaetic of Württemberg. In 1857<sup>2</sup> Falconer described the first Jurassic form, *Plagiaulax*. Even in 1871, when Owen’s great memoir was published, the existence of the group as such was not clearly understood. His arrangement was, briefly, as follows:

Marsupialia	{	More than two lower incisors.	{	More than the type number of molars.	{	<i>Microlestes</i> and many genera of other orders.
				Type number of molars.		Three tri-conodonts
	{	Not more than two lower incisors.	{	Less than type number of molars	{	<i>Plagiaulax</i>

Incertae sedis: *Stereognathus*, *Bolodon*.

Owen applied no names of families to the Mesozoic mammals. The earliest names of this sort are to be found in Murray (1866, p. 364) who includes in his systematic table the following undefined and entirely unnatural families:

Stereognathidae:

*Stereognathus*, *Pliolophus*.

<sup>2</sup> For these and all other references throughout the memoir consult the bibliography at the end.

Microlestidae:

*Thylacotherium* (*Amphilestes*), *Thylacotherium* (*Amphitherium*), *Microlestes*, *Spalacotherium*, *Plagiaulax*, *Triconodon*, *Dromatherium*, *Galethylax*, *Spalacodon*.

As with Owen's later tabulation, the genera now referred to the Multituberculata were by Murray separated widely. His Microlestidae contained all the Mesozoic mammals then known, except *Stereognathus*, and also contained two quite unrelated Eocene forms.

Gill (1872) made *Plagiaulax* the type of the distinct family Plagiaulacidae and Owen in 1885 recognized, at least by implication, the present accepted limits of the group which he had severed so widely fourteen years earlier, now comparing *Plagiaulax*, *Neoplagiaulax*, *Tritylodon*, and *Microlestes*. The credit for the first clear statement uniting the genera of multituberculates into a unit is, however, due to Marsh. In 1880 he stated, "Another order of Mesozoic mammals is evidently represented by *Plagiaulax*, the allied genus *Ctenacodon*, and possibly one or two other genera. These are chiefly specialized aberrant forms, which apparently have left no descendants. This order, which may be termed the *Allotheria*, can be distinguished from the previous group [Pantotheria] by the following characters:

1. Teeth much below normal number.
2. Canine teeth wanting.
3. Premolar and molar teeth specialized.
4. Angle of lower jaw inflected.
5. Mylohyoid groove wanting.

"The characters above do not indeed separate the Plagiaulacidae from some of the marsupials and future discoveries may prove them to belong to that group, where they would then represent a marked suborder."

In view of later criticisms of this definition, it may be well to point out, first, that Marsh was dealing only with Jurassic mammals and that his definition was, as he clearly states, meant to distinguish the *Allotheria* from other Jurassic mammals, which it does, and second, that it is an ordinal definition and does separate the multituberculates adequately from the Marsupialia as an order.

In 1887 Marsh repeated this definition, mentioning "*Allodon*, *Bolodon*, *Ctenacodon*, *Plagiaulax*, and a few other genera." He also mentioned the Microlestidae as members of the group, but he then definitely placed the *Allotheria* in the Marsupialia.

Meanwhile, in 1884, Cope had published his paper on Tertiary marsupials, in which he stated, "The extinct marsupials belong to three types, as distinguished by the form of the superior molar teeth. These are trituberculate, quadrituberculate, or multituberculate. . . . The third division is entirely distinct and is characterized by having at least three longitudinal series of tubercles in its superior molar teeth. To this suborder I apply the name Multituberculata." Although often accepted in place of *Allotheria* on the grounds that the latter was not really defined, the original definition of Multituberculata is seen to be erroneous, for no multituberculate has more than three rows of tubercles on the upper molars and many have only two.



Cope included three families in his suborder: Tritylodontidae, Polymastodontidae, and Plagiaulacidae. In 1887 he added the Chirogidae, based on the genus *Chirox* and supposedly intermediate between the Plagiaulacidae and Polymastodontidae.

Osborn's classification of 1888 (1888A) may be summed up as follows:

[Order Marsupialia]

Suborder Multituberculata

Plagiaulacidae

*Microlestes*, *Ctenacodon*, *Plagiaulax*, *Ptilodus*, *Neoplagiaulax*,  
*Meniscoëssus*, "and perhaps also *Thylacoleo*."

Bolodontidae

*Bolodon*, *Allodon*, and possibly *Chirox*.

Tritylodontidae

*Tritylodon*, *Triglyphus*.

Polymastodontidae

*Polymastodon*

*Incertae sedis*: *Stereognathus*.

In 1889 Marsh proposed several new families for Lance (upper Cretaceous) genera: Cimolodontidae, Dipriodontidae, Tripriodontidae, Cimolomidae. He also stated that one form belonged to "the family named by the writer, the Allodontidae." The latter family had not, however, been previously mentioned. It was apparently advanced on grounds similar to those for the Chirogidae and Bolodontidae, with which it was probably meant to be synonymous. In 1887 Marsh had definitely stated that *Allodon* belonged to the Plagiaulacidae, and the retreat implied in 1889 was, as time has shown, an unfortunate step away from the true expression of relationships.

In his first review of Marsh's work, Osborn placed the Cimolomidae and Cimolodontidae in the Plagiaulacidae. He also erected the family Stereognathidae "distinguished by the presence of two rows of tubercles in the upper molars and three in the lower, of the crescentoid pattern" to include the Dipriodontidae and Tripriodontidae, as well as *Stereognathus* itself. In his later work on Lance mammals, however (1894), Osborn abandoned this modification of his familial classification, recognizing its erroneous basis and referring all upper Cretaceous multituberculates to the family Plagiaulacidae.

In their joint paper on the mammals of the Puerco (1895) Osborn and Earle proposed dividing the Plagiaulacidae into the two subfamilies Plagiaulacinae and Polymastodontinae, which they defined.

Finally, in 1909, Gidley showed that *Chirox* was based on the upper jaw of *Ptilodus*. Although he did not redefine the families, it obviously followed that the families Chirogidae, Allodontidae, and Bolodontidae were invalid.

By the steps now very briefly recapitulated, there has been achieved a twofold or threefold division of the order. Typical of recent views is that given by Schlosser in the 1923 edition of the Zittel *Grundzüge*:



Mammalia  
 Eplacentalia  
   Order Marsupialia  
     Suborder Allotheria  
       Tritylodontidae  
       Plagiaulacidae  
       Polymastodontidae  
       Polydolopidae<sup>3</sup>

In the course of the present and of related studies, all the pertinent materials have been restudied at first hand. The results are given in large part in the present memoir and completed in the various papers bearing on multituberculates given in the appended bibliography under Simpson, and Granger and Simpson. On these results is based the following synoptic classification of the multituberculates:

CLASS MAMMALIA Linnaeus 1758  
 SUBCLASS ALLOTHERIA Marsh 1880, emend. Simpson 1928<sup>4</sup>  
 ORDER MULTITUBERCULATA Cope 1884<sup>5</sup>  
   SUBORDER TRITYLODONTOIDEA Simpson 1925  
     Family Tritylodontidae Cope 1884  
       *Tritylodon* Owen 1884  
       *Oligokyphus* Hennig 1921  
       *Chalepotherium* Simpson 1928  
       *Stereognathus* Charlesworth 1855  
       *Inc. sed.: Archaeodon* v. Huene 1925  
   SUBORDER PLAGIAULACOIDEA Simpson 1925  
     Family Plagiaulacidae Gill 1872  
       *Plagiaulax* Falconer 1857  
       *Bolodon* Owen 1871  
       *Ctenacodon* Marsh 1879  
       *Psalodon* Simpson 1926  
       *Loxaulax* Simpson 1928  
     Family Ptilodontidae Simpson 1925  
       *Ptilodus* Cope 1881  
       *Neoplagiaulax* Lemoine 1882  
       *Liotomus* Cope 1884

<sup>3</sup> Although usually placed in the Multituberculata, the polydolopids surely do not belong here as the writer has elsewhere attempted to prove (Simpson 1928E). A discussion of them is not necessary in this work.

<sup>4</sup> Proposed by Marsh as an order, afterward reduced by him to subordinal rank. Granger (1915) suggested that the multituberculates "are probably entitled to rank as a distinct primary division [i.e., subclass] of the Mammalia." The present writer proposes to retain the generally adopted term Multituberculata for the order and to use Allotheria for the subclass, a use for which its form is very apt.

<sup>5</sup> Proposed as a suborder, afterward raised to ordinal rank.

## AMERICAN MESOZOIC MAMMALIA

- Eucosmodon* Matthew & Granger 1921  
*Ectypodus* Matthew & Granger 1921  
*Prionessus* Matthew & Granger 1925  
*Paronychodon* Cope 1876<sup>6</sup>  
*Meniscoëssus* Cope 1882<sup>6</sup>  
*Dipriodon* Marsh 1889<sup>6</sup>  
*Cimolodon* Marsh 1889  
*Cimolomys* Marsh 1889  
*Essonodon* Simpson 1927  
*Djadochtatherium* Simpson 1925  
 Family Taeniolabididae Granger & Simpson 1929  
*Taeniolabis* Cope 1882  
*Catopsalis* Cope 1882  
*Incertae sedis*:  
 Family Microcleptidae Simpson 1928  
*Microcleptes* Simpson 1928  
*Thomasia* Poche 1908  
 Inc. sed.: *Hypsiprymnopsis* Dawkins 1864

The suggested relationships of the various larger groups are as follows:



Only the families Plagiaulacidae and Ptilodontidae of the suborder Plagiaulacoidea occur in the American Mesozoic.

<sup>6</sup> On the validity of these three genera, see below.

SUBORDER *PLAGIAULACOIDEA* Simpson 1925

DEFINITION.—Molars two in number, the first, at least, elongated. The lower molars with two and the upper molars with two or three longitudinal rows of two to twelve cusps each. Premolars sharply differentiated from molars, the posterior ones forming a strong shearing device, secondarily lost in the Taeniolabididae. The lachrymal reduced or absent, the jugal and frontal much reduced, with progressive overlapping of the latter by the parietal. Zygomatic process of maxilla strong, with a squamosal contact. Palate usually broad, extending back to end of molar series, with or without vacuities.

This suborder is practically coextensive with the family Plagiaulacidae of some authors, but its right to rank as a suborder can hardly be disputed if the same criteria are applied as are used in classifying Tertiary and recent mammals. From a strictly Linnaean (or static) point of view, its morphological variety and distinctness is as great as in the average suborder of conservative recent classifications, and from a phylogenetic (kinetic) point of view, the relative time of its known emergence, the number of included phyla, and the plan and scope of its development also fully warrant its subordinal separation. There is a human tendency to lump together under a few easily remembered names a number of really quite diverse units when the latter are not well known to the individual taxonomist. There is also, of course, the tendency of the specialist to multiply terms and to give his own groups a high status which would be impractical in a more general view of the class, but the Mesozoic mammals have certainly suffered from the former tendency and not from the latter. Recording, as they do, twice as long a period of evolution as the Tertiary mammals, they are worthy of emphasis, and, as this memoir is intended in part to reveal, their remains although scanty and imperfect are more characteristic than is generally believed. All that is asked is that some approach be made toward applying to them the same taxonomic standards as are applied to other mammals.

Four families are provisionally referred to the Plagiaulacoidea. One, the Microcleptidae,<sup>7</sup> is wholly doubtful as to the affinities and is placed here only provisionally. The Taeniolabididae ("Polymastodontidae"), recognized as a family by Cope and still often so classified, were reduced to subfamilial rank by Osborn. The group is now recognized as a family, but it is exclusively Paleocene and is not here treated. There remain a number of upper Jurassic, Cretaceous, Paleocene, and Eocene genera which have hitherto, almost without exception, been retained by all in the family Plagiaulacidae, and even in a single subfamily Plagiaulacinae. They include, however, two quite distinct groups, one upper Jurassic and lower Cretaceous in age and typified by *Plagiaulax* and *Ctenacodon*, the other ranging from upper Cretaceous into the Eocene and typified by *Ptilodus*. These may be contrasted as follows:

<sup>7</sup> Microlestidae of earlier workers. The generic name *Microlestes* was preoccupied when applied to a member of this group. See Simpson 1928a.



*Ctenacodon* and its allies.

1. Upper premolars 5, simpler.
2.  $P^{4-5}$  shearing.
3. Lower premolars 3-4,  $P_4$  with 5-8 serrations.
4.  $M_1^1$  and  $M_2^2$  subequal.
5.  $M^{1-2}$  with two rows of cusps.
6. 2-4 cusps in each row on molars.
7. Molar cusps simple and nearly conical.

*Ptilodus* and its allies.

1. Upper premolars 4-3, may be more complex.
2. Only last upper premolar shearing.
3. Lower premolars 1-2,  $P_4$  with 6-14 serrations.
4.  $M_1^1$  much larger than  $M_2^2$ .
5.  $M^{1-2}$  with three rows of cusps.
6. Molar cusps more numerous.
7. Molar cusps more or less crescentic and generally complicated by other ridges and grooves.

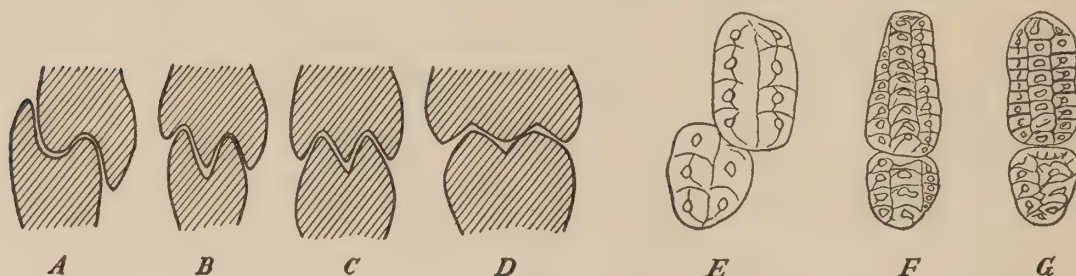


FIG. 3. Diagram illustrating evolution of plagiaulacoid molars. A-D, transverse sections of molars in occlusion. A, Plagiaulacidae. B, Ptilodontidae, more primitive stage. C, Ptilodontidae, more advanced stage. D, Taeniolabididae (somewhat worn). E-G, crown views of left upper molars. E, *Ctenacodon*. F, *Cimolomys*. G, *Taeniolabis*. Not to scale.

As has long been held, these differences are mainly such as could be imputed to evolutionary advance in the interval between the earliest Cretaceous and the upper Cretaceous. Nevertheless it is apparent that the morphological break is great and that the differences are at least as marked as those used to separate allied families among later mammals. Such a feature as the presence of two subequal upper shearing teeth in the earlier forms and only one enlarged shearing tooth preceded by smaller grasping teeth in the later ones may indicate that the relationship is not a directly ancestral one. In any event our present knowledge requires their separation into two families. For the earlier group the name Plagiaulacidae, in a restricted sense, is retained. The later group is named Ptilodontidae, after its best known and most typical genus.

In the present section we are concerned only with the American Plagiaulacidae. The Mesozoic Ptilodontidae will be discussed below in treating the faunas of the upper Cretaceous.

## PLAGIAULACIDAE Gill 1872

DEFINITION.—Premolars five above and four or three below, the lower premolars shearing inside the subequal last two upper ones. Molars, upper and lower, all of about



the same size and each with two rows of cusps, with not over four cusps in any one row. Molar cusps not definitely crested or truly crescentic.

TYPE.—*Plagiaulax* Falconer.

DISTRIBUTION.—Purbeckian (upper Jurassic) and Wealden (lower Cretaceous) of England, Morrison (upper Jurassic) of Wyoming.

In this family the genera *Plagiaulax*, *Bolodon*, *Ctenacodon*, *Psalodon*, and *Loxaulax* are now recognized. All but *Psalodon* occur in England, only *Ctenacodon* and *Psalodon* in America. *Loxaulax* is a Wealden form; the others are from the English Purbeck or American Morrison. *Bolodon* is based on upper jaws, of which three species are known in the Purbeckian, and it probably is synonymous with or includes species of *Plagiaulax* and (or) *Ctenacodon*, but it must be retained provisionally until its association with lower jaws shall have been demonstrated. *Plagiaulax* is known, as such, only from lower jaws. The type of *Psalodon* is an upper jaw, but a lower jaw is referred. The type of *Ctenacodon* is a lower jaw, but an upper jaw is referred.

The following table gives in *résumé* the present disposition of the American members of the family:

Marsh 1887	Present Memoir
<i>Ctenacodon serratus</i> }	..... <i>Ctenacodon serratus</i> Marsh
<i>Ctenacodon nanus</i> }	
	<i>Ctenacodon scindens</i> Simpson
<i>Allodon laticeps</i> .....	<i>Ctenacodon laticeps</i> (Marsh)
<i>Ctenacodon potens</i> .....	<i>Psalodon potens</i> (Marsh)
<i>Allodon fortis</i> .....	<i>Psalodon fortis</i> (Marsh)
	? <i>Psalodon marshi</i> Simpson

Owing to the lack of association of the various parts of the dentition, this list includes several possible synonyms. *Psalodon* and *Ctenacodon* are surely distinct, but *Ct. laticeps* may be the upper dentition of *Ct. serratus*, and *Ps. fortis*, *Ps. potens*, and *Ps. marshi* may be respectively the anterior upper, posterior upper, and lower teeth of the same species. If these possibilities should materialize, the list would be reduced to *Ctenacodon serratus*, *Ctenacodon scindens*, and *Psalodon potens*.

#### *Ctenacodon* Marsh 1879

1879. *Ctenacodon*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 396.

1881. *Allodon*, Marsh, *Amer. Jour. Sci.* (3) XXI, 511.

1884. *Pliopriion*, Cope, *Am. Nat.*, XVIII, 691.

DEFINITION.—Four lower premolars. P<sub>2</sub> shearing, with or without serrations, relatively larger than in *Plagiaulax*. Ridges on shearing teeth confined to part near edge. Jaw longer and more slender than in *Plagiaulax*. P<sup>3</sup> with three subequal cusps. P<sup>4</sup> broad, with three outer and four inner cusps, P<sup>5</sup> similar but with two outer cusps. Outer cusps well developed.

TYPE.—*Ct. serratus* Marsh.

DISTRIBUTION.—Purbeckian, England; Morrison, Wyoming.

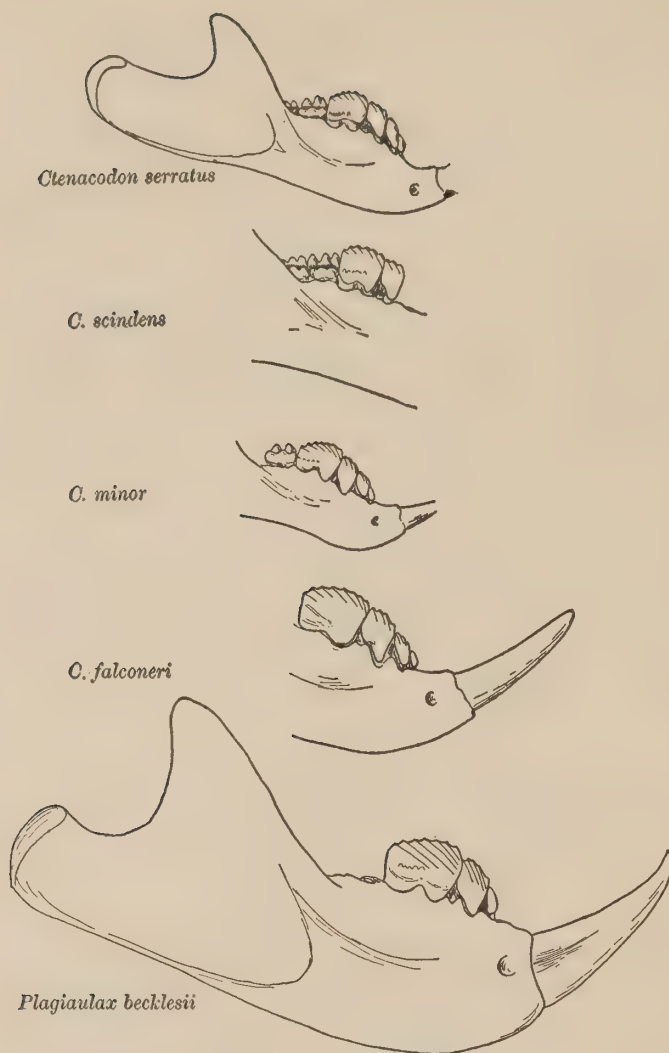


FIG. 4. *Ctenacodon* and *Plagiaulax*. Comparison of American and European species. Right lower jaws, external views. Three times natural size. (From Simpson, 1928B.)

*Ctenacodon* and *Plagiaulax* are closely related and have, indeed, sometimes been considered to be synonymous. It has elsewhere been shown, however, that *Ctenacodon serratus* and *Plagiaulax becklesii* belong in different genera (Simpson 1928B). *Plagiaulax* has no  $P_1$ ,  $P_2$  is relatively smaller and simpler, the ridges on the shearing teeth extend far down on the sides, and the jaw is relatively shorter and stouter. "*Plagiaulax*" *minor* Falconer and "*P.*" *falconeri* do not belong to *Plagiaulax*, as was first recognized by Cope who placed them in a new genus, *Plioprion*. *Plioprion* proves, however, to be inseparable from *Ctenacodon*, which thus includes four species based on lower jaws. The two English species, *Ct. minor* and *Ct. falconeri* resemble one another somewhat more closely than they do the American species, and the same is true of the latter, *Ct. serratus* and *Ct. scindens*, with respect to the English species.  $P_4$  is larger relative to  $P_3$  in the English species and they also have a slightly

greater number of serrations on the shearing edges of these teeth, apparently indicating that these forms are somewhat more advanced than the American ones.

#### *Ctenacodon serratus* Marsh 1879

1879. *Ct. serratus*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 396.

1881. *Ct. nanus*, Marsh, *Amer. Jour. Sci.* (3) XXI, 512.

TYPE.—Cat. No. 11833, Yale Peabody Museum. Right lower jaw, free of matrix, lacking  $M_2$  and extreme anterior and posterior parts of ramus. Fig'd, Marsh 1887, Pl. VIII, fig. 1.

TYPE OF *CT. NANUS*.—Cat. No. 11832, Y.P.M. Left lower jaw with  $P_{1-4}$  and  $M_{1-2}$ .

PRINCIPAL REFERRED SPECIMENS.—Cat. No. 13668, Y.P.M. Left lower jaw in matrix, inner aspect, complete save for tip of coronoid, incisor, and molars. Fig'd, Marsh 1887, Pl. VII, fig. 4.

Cat. No. 2688, U.S.N.M. Lower jaw with  $P_{1-4}$  well preserved and little worn.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Length  $P_{1-4}$ , about 4.2 mm. Length ratio  $P_4 : P_3$ , 1.54. Three serrations on edge of  $P_3$  and six on  $P_4$ .  $P_4$  lower relative to its length than in *C. scindens*. Anterointernal cusp of  $M_1$  small and not very distinct.

The following characters were supposed by Marsh to be distinctive of his species *C. nanus*:

1. "The last premolar only has its summit marked by faint notches."
2. "The ridge starting at the base of the coronoid and extending forward on the outer side is much sharper than in the larger species."
3. The following comparable measurements are given:

	<i>C. serratus</i>	<i>C. nanus</i>
Space occupied by $P_{1-4}$	4.5 mm.	4.0 mm.
Height of $P_4$	1.5 mm.	1.25 mm.

The first character was not given diagnostic value, and reëxamination shows that it is accidental, the summit of  $P_3$  being broken in the type of *C. nanus*. The second character is not confirmed by simultaneous study of the two specimens under the binocular microscope. New measurements (see below) show the difference in size of teeth to be so slight that it certainly is not of specific value in itself. The jaw of *C. nanus* is about 13 per cent smaller, but this is due in large part to its being a younger individual, possibly also to sexual difference. The general agreement is so close that both species cannot be maintained.

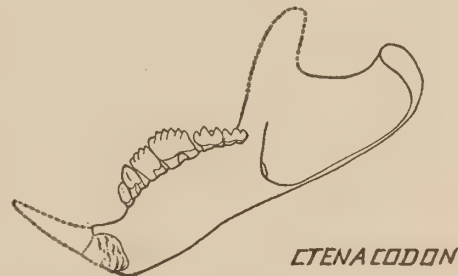


FIG. 5. *Ctenacodon*. Diagrammatic internal view of right lower jaw. Three times natural size.

#### DENTITION

The dental formula is clearly  $I_1 C_0 P_4 M_2$ . The incisor is not known in association, but, from its alveolus, it was a simple, large, curved tooth of oval section. It is followed by a short diastema back of which are the four premolars, forming together a compressed wall. The first premolar hardly joins in the shearing edge. It is small and low and rises to a single point which nearly touches the somewhat overhanging anterior portion of the succeeding tooth. It is implanted by two subequal roots and has a swollen base, almost circular in horizontal section.

The second and third lower premolars are much alike, save that the third is



larger. Each is implanted by two subequal roots, each is swollen at the base of the crown, and each presents a flat oblique surface externally and another internally, the two meeting at the crest and forming a sharp anteroposterior ridge. To think of the teeth as a whole as compressed is a little misleading, for the swollen base is so much wider than roots or crest that the maximum width of  $P_2$  is actually greater than its length and in  $P_3$  these dimensions are nearly equal. The external face continues downward anteroexternally and forms a small projecting process outside the anterior root. The crest of  $P_3$  has three notches and four small angular projections. The posterior three projections correspond with three low ridges which run obliquely downward and somewhat forward on the lateral faces of the tooth, becoming obsolete not far from the edge.

$P_4$  is nearly twice as long as  $P_3$  and is implanted by two stout roots of which the posterior is the larger. The width is about that of  $P_3$ . The chisel-like edge, instead of being inclined downward and forward at about  $45^\circ$  as in the two preceding teeth is nearly horizontal, although the anterior portion curves downward somewhat in transition to the more oblique preceding crest. The serrations of the edge are six in number, and the lateral ridges five. In U.S.N.M. No. 2688, which is almost unworn, there is plainly an outer row of small accessory basal cusps on  $P_4$ , such as is described in more detail below for *?Psalodon marshi*. This peculiar feature apparently occurred in all plagiaulacids.

It is customary to speak of the shearing edge of the premolars as curved, but closer analysis shows that it can better be described as forming two straight lines meeting at an angle. The shorter, more posterior line is horizontal and comprises most of the edge of  $P_4$ , while the longer one is inclined at about  $45^\circ$  and comprises  $P_{1-3}$  and the anterior end of  $P_4$ . The mechanical advantage of such an arrangement, working up and down and also back and forth against a shorter, horizontal upper blade is apparent.

In the type,  $M_1$  is worn and  $M_2$  absent. In Y.P.M. No. 11832,  $M_1$  is less worn and  $M_2$  is preserved, although slightly broken. Comparison of these specimens and of all the other available material, much of which is excellently preserved, shows that these teeth are very unlike the earlier descriptions of them. The discrepancies, however, are easily explained by the fact that these molars are very seldom preserved and even when present are usually badly worn. Viewing worn materials with a hand lens and without unworn teeth for comparison, the number of cusps in a single row may often appear to be five or six. There is, however, no doubt at present that there never occur more than three in lower molars of *Ctenacodon*, at least. When worn a pit appears in the dentine at the apex, giving the appearance of two cusps where but one really occurred.  $M_1$  has six cusps arranged in two rows of three each. The outer cusps are lower and suffer most from wear. The anteroexternal cusp is about half the size of the second, and the second and third are about equal. The inner cusps are wholly internal to the cusps of  $M^1$  in occlusion and consequently are always less worn. The second and third cusps are equal and are separated by a deep notch. The anterointernal cusp is small and is poorly separated from the second, appearing to be developed on the anterior slope of the latter. Moderate wear may cause it to lose its individuality, so that there may appear to be only two internal cusps.

$M_2$  is a little broader than  $M_1$ , but it also has six cusps in two rows of three each. These cusps all appear to be of about the same size on this tooth. Both molars are implanted by two stout roots, each slightly compressed anteroposteriorly. The roots are developed vertically to the alveolar border, which is oblique, while the crowns are horizontal. Consequently the roots are obliquely affixed to the crowns.

#### MANDIBLE

The mandible turns inward quite sharply anteriorly at the symphysis. The symphyseal surface is short, not quite extending back to a vertical line anterior to  $P_1$ . There is a single mental foramen beneath the diastema. When the jaw is oriented with the grinding surface of the molars horizontal, the mandible is oblique, the anterior portion much lower than the posterior. Beneath  $P_2$  there starts a slight ridge, much emphasized by Marsh, which curves backward on the external face of the mandible and passes into the anterior border of the coronoid. The latter arises external to  $M_2$  and is rather weak and short.<sup>8</sup> A number of misapprehensions have arisen with regard to the posterior part of the mandible. Marsh represented it (1887, Pl. VIII, fig. 4) as having a distinct inflected angle, and he considered the distinctness of the angle to be in contrast with *Plagiaulax*. Reëxamination shows that the original is slightly crushed and that careful reconstruction gives a condition exactly like that in other multituberculates. There is no proper angular process, only a well developed pterygoid crest running forward from the articular condyle. On the opposite side (outside) of the jaw is a somewhat similar but less prominent, efflected masseteric crest. The dental foramen is at the anterior end of the pterygoid fossa, just posterior to the roots of  $M_2$ . The condyle is not separated by a restriction from the rest of the mandible. The articular surface looks upward and backward. It has a broad, gently convex superior surface, for grinding, and a short, more sharply convex, posterior area, used in opening and closing the mouth.

#### MEASUREMENTS

The unusual orientation of these jaws makes the selection of useful standard coördinates difficult. The following tooth measurements are maximum lengths taken along the inclined alveolar border. All measurements in this memoir are in millimeters.

	$P_1-M_2$	$P_{1-4}$	$M_{1-2}$	$P_1$	$P_2$	$P_3$	$P_4$	$M_1$	$M_2$
Y.P.M. 11833	6.7	4.2	2.7	0.5	1.0	1.1	1.7	1.3	ca. 1.4
Y.P.M. 11832	6.5	4.1	2.5	0.5	0.8	1.1	1.6	1.1	1.3
Y.P.M. 13668	ca. 6.9	4.3	ca. 2.7	0.6	0.9	1.2	1.7	..	..
U.S.N.M. 2688	..	4.0	..	0.6	0.9	1.1	1.6	..	..

<sup>8</sup> Marsh's original figure (see 1887, Pl. VIII, fig. 1) restored the posterior part of the mandible before it was adequately known and is incorrect in many particulars, as may be seen by comparing with his Pl. VIII, fig. 4 and with the present figures. In Pl. VIII, fig. 4, the angle is incorrectly shown and the figure is inadvertently labeled "x3," whereas it is actually x4.

	Shortest distance from alveolus of $P_4$ to lower border	Anterior end of symphysis to posterior end of condyle
Y.P.M. 11833	3.7	..
Y.P.M. 11832	3.2	..
Y.P.M. 13668	3.7	17.3

*Ctenacodon scindens* Simpson 1928

1928. *Ct. scindens*, Simpson, *Cat. Mes. Mam.* . . . *Brit. Mus.*, p. 36.

TYPE.—Cat. No. 10366, Y.P.M. Part of left lower jaw, free of matrix, with  $P_{3-4}$ ,  $M_{1-2}$  and roots of  $P_{1-2}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Length  $P_{1-4}$  about 4.6 mm. Length ratio  $P_4 : P_3$ , 1.82. Premolar serrations as in *Ct. serratus*.  $P_4$  higher relative to length than in other known species. Anterointernal cusp of  $M_1$  larger than in *Ct. serratus*.

## DENTITION

The two premolars preserved are identical in pattern with those of *Ctenacodon serratus*, but differ in proportions. Both are higher relative to their lengths than in the genotype, and  $P_3$  is shorter relative to  $P_4$ .

$M_1$  has the anterointernal cusp better developed than in the preceding species, although it is less distinct from the second internal cusp than is the third. The external row is of three rounded and much worn cusps, the anterior the smallest, as before.  $M_2$  is broader and more rounded in outline than  $M_1$ . The inner cusps are separated by deep notches, although here it is the second notch and not the first which is shallower. There are three subequal outer cusps.

The dental series as a whole is about 12 per cent or more larger than in *Ct. serratus*, but it is somewhat smaller in proportion to the depth of the jaw.

## MANDIBLE

The lower jaw was apparently shorter and heavier in proportions than in the type species. The outer ridge alluded to in the description of the latter is here much less marked and is scarcely to be distinguished until it rises to form the anterior border of the coronoid.

## MEASUREMENTS

All measurements from the type:

Lengths:

$P_1-M_2$	7.5	$M_1$	1.5
$P_{1-4}$	4.6	$M_2$	1.5
$M_{1-2}$	3.0	Shortest distance	
$P_1$	0.6	from alveolus of $P_4$	
$P_2$	1.0	to lower border	4.3
$P_3$	1.1		
$P_4$	2.0		



*Ctenacodon laticeps* (Marsh 1881)

1881. *Allodon laticeps*, Marsh, *Amer. Jour. Sci.* (3) XXI, 511.

1927. *Ctenacodon laticeps*, Simpson, *Amer. Jour. Sci.* (5) XIV, 37.

TYPE.—Cat. No. 11761, Y.P.M. Part of left maxilla with P<sup>1-5</sup> and M<sup>1-2</sup>. Fig'd, Marsh 1887, Pl. VII, figs. 1-2.

PRINCIPAL REFERRED SPECIMENS.—U.S.N.M. No. 2681. Part of left maxilla with P<sup>1-4</sup>. Fig'd, Marsh 1887, Pl. VII, figs. 3-4.

U.S.N.M. No. 2682. Part of left maxilla with P<sup>4-5</sup> and M<sup>1</sup>. Fig'd, Marsh 1887, Pl. VII, figs. 5-6.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Based on upper jaws possibly belonging to *Ctenacodon serratus*, and including all the upper jaws probably referable to *Ctenacodon*. Length of premolar series about 4.5 mm.

The genus *Allodon* was originally founded on its possession of five premolars, supposedly distinguishing it from *Ctenacodon* with only four lower premolars. In 1887 Marsh recognized the weak point of this definition and inferred that *Allodon* had only four lower premolars, like *Ctenacodon*. At this time he also founded a second species of the supposed genus, *Allodon fortis* "three or four times as large as *Allodon laticeps*." This second species was based on a premaxilla, and had no parts which could be directly compared with the genotype. Its reference to the supposed genus was therefore entirely by inference, the basis for which is not now clear. From the character of I<sup>2</sup> in this premaxilla he inferred that the lower incisor must be gliriform, with a chisel-like end, and he figured an isolated tooth supposed to show this character. This was supposed to substantiate the difference between *Allodon* and *Ctenacodon*. The weakness of this position is apparent from the standpoint of present work although, historically considered, Marsh's course was much nearer the truth than that of many later workers. In the first place, there was no real evidence that

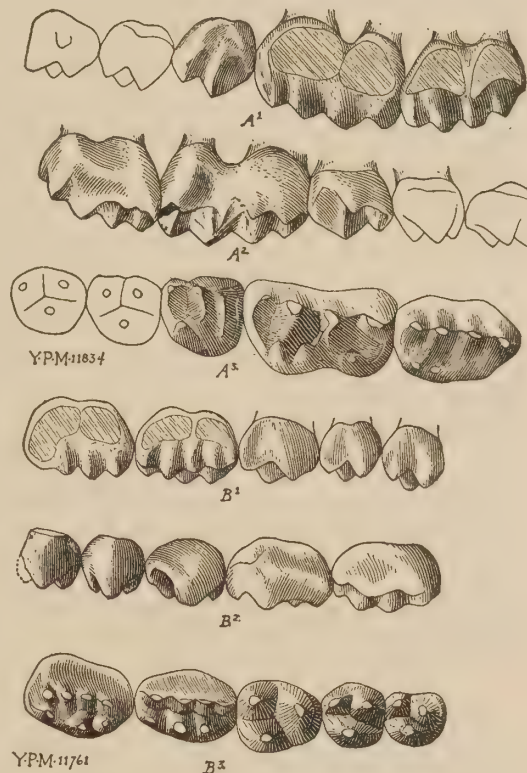


FIG. 6. Upper premolars of American plagiaulacids. A, *Psalodon potens*, type, right upper jaw. A¹, internal. A², external. A³, crown. B, *Ctenacodon laticeps*, type, left upper jaw. B¹, internal. B², external. B³, crown. A, 7½ times natural size. B, 12½ times natural size.

the premaxilla did belong to *Allodon*, and in the second place, it has since been found that the type of  $I^2$  in this jaw does *not* require a rodent-like lower incisor and that the referred lower incisor is simply a broken tooth of the same type as that found in *Ctenacodon*, *Plagiaulax*, and probably all plagiaulacids. Marsh further found support for his position at that time in the existence of large lower jaws with normal incisors. He naturally referred these to *Ctenacodon* (*Ct. potens*), being of the opinion that they could not belong with the premaxilla referred to *Allodon*. He also found large upper jaws, suited in size to belong either with "*Allodon*" *fortis* or with the large lower jaws referred to *Ctenacodon*. Since they differed from "*Allodon*" *laticeps* in generic characters, he naturally referred them to *Ctenacodon*, basing the species *Ct. potens* upon them. This conclusion, apparently logical at the time, also had a double weakness, however, for it was not true that the large lower jaws could not go with the premaxilla, and it was not true that the premaxilla necessarily belonged in the same genus as "*Allodon*" *laticeps*. Hence there was, actually, no reason why these three parts of large dentitions, of a size suitable to represent a single species, should not have been placed together. In fact all later work seems to indicate that they did belong together.

Marsh himself had found that the original generic character supposed to separate *Allodon* and *Ctenacodon* was incorrect, and it has just been shown that the additional evidence submitted in 1887 also failed to indicate that *Allodon* and *Ctenacodon* were distinct. "*Allodon*" *laticeps* is suitable in every way to be the upper dentition of *Ctenacodon serratus*. The teeth occlude perfectly, and there is now no evidence against this view. Until upper and lower teeth are actually found in association, it is convenient and justifiable to retain Marsh's trivial name *laticeps*, but there can be little doubt that it should be referred to *Ctenacodon*.

Turning from these relatively unimportant matters of nomenclature, it will be seen that Marsh was in 1887 many years ahead of contemporary thought in his conception of the true characters of the plagiaulacids, for he insisted that the upper jaws of *Allodon* type were closely related to the lower jaws of *Ctenacodon* type. Cope and later Osborn, on the other hand, placed these upper and lower jaws in different families, Plagiaulacidae for the lower and Bolodontidae or Chirogidae for the upper teeth. So cogent were the arguments which they advanced that Marsh himself finally abandoned his correct view and proposed a family Allodontidae, as already mentioned. It was not until Gidley's description of the full dentition in *Ptilodus* (1909) that Marsh's first opinions were fully vindicated.

#### DENTITION

The dental formula is  $I^{?3} C^0 P^5 M^2$ . This formula, although often accepted, has been subjected to much criticism and requires defense. The incisors are not known, but they must have been much as in *Bolodon* or *Psalodon*, both of which have three pairs. Marsh stated that there was in the type (Y.P.M. No. 11761) an alveolus anterior to the preserved premolars in the maxilla and lodging originally either another premolar (making six) or a canine. There is such an alveolus, but it is strongly inclined forward and the alveolar border is here broken away. If the alveolar border were restored



the opening of the alveolus would be in advance of the maxillo-premaxillary suture. This would be at least anomalous for a premolar or canine, but it would be entirely normal for an incisor. The roots of enlarged incisors often extend back into the maxilla. Comparison with *Psalodon* and with *Bolodon*, both very closely related, leaves little doubt that there was no canine and that there were only five premolars.

The next question is that of the division of the seven cheek teeth into premolars and molars. Marsh's view, supported by Gidley and others, was that there were five premolars (reduced in number in the Cretaceous and Paleocene multituberculates) and two molars (constant for the suborder Plagiaulacoidea). Osborn (1888A) suggested a formula of  $P^3 M^4$  for *Bolodon*. Broom (1914) recognized the possibility of this, but considered  $P^4 M^3$  as probable for *Bolodon* and *Ctenacodon*. The whole question is a complex one, and it has been treated in a general way elsewhere, so that a brief *résumé* must here suffice. Broom especially was probably influenced by the desire to give *Ctenacodon* a normal mammalian dental formula. The fact is that *Ctenacodon* is not a "normal mammal." It is removed by millions of years from the first mammals with a fixed formula of either  $P^3 M^4$  or  $P^4 M^3$ , and as Broom himself has conclusively shown, it is not related to these mammals. Analogy with forms so far removed in time and in zoölogical relationships must surely be an uncertain guide. If the morphology of the teeth themselves were amenable to such interpretation, it would be gladly accepted, but this is not the case. The fourth and fifth upper cheek teeth are almost identical in structure, in function, and in degree of wear in the known specimens. It is logically impossible to refer them to different dental series; the formula must be either  $P^3 M^4$ , as given by Osborn, or  $P^5 M^2$ , as given by Marsh. Now, the fourth and fifth upper cheek teeth do not have the same structure as the two which follow. The latter are grinding teeth (literally "molars") with two straight longitudinal rows of cusps separated by a straight valley, while the former are grasping and shearing teeth, with conical, rugose cusps arranged roughly in two rows but not adapted to fore-and-aft motion, in other words exactly like the teeth which precede them except for having two or three more cusps. Furthermore they act against the lower shearing teeth or premolars.<sup>9</sup> Their consideration as anything but premolars could only be justified in the present state of our knowledge by actual demonstration of the extent of tooth replacement in these genera. This is not now forthcoming, and it would be surprising, although of course not impossible, if it ran counter to the morphological facts.

A few other formulae have been assigned to this group, such as  $I_1^1 C_0^1 P_4^4 M_3^3$ ,<sup>10</sup> but they are hardly worthy of more extended discussion.

The first three premolars are identical in pattern and of almost the same size, although the second and third are progressively a little smaller. Each has three low

<sup>9</sup> Broom divides the lower shearing teeth also, considering the last one or two as molars. Without depreciating Broom's ingenious argument (1914, p. 121), study of the illustrations here given will show at once that this view does violence to the known morphology. It can only be maintained by having recourse to analogies which are either doubtful or demonstrably incorrect.

<sup>10</sup> Schlosser in Zittel's *Grundzüge*, 1923. This is for *Plagiaulax* and gives that genus two more teeth in the lower jaw than it actually possesses, deprives it of two of its upper incisors, gives it a canine of which there is no trace, and adopts an untenable division of the premolar-molar series.



conical cusps, two internal and one external, the latter a little larger and slightly posterior to the middle of the tooth. All of these cusps are marked by light radial furrows when unworn. Although low, the cusps have sharp points and there is a rather insignificant sharp ridge running down the anterointernal cusp and up the postero-internal one, and another similarly uniting the postero-internal and external cusps.

The cusps of  $P^4$  are the same low circular cones, and there is again no definite longitudinal valley, but the number of cusps is higher. There is an outer row of three cusps, the middle the largest and posterior the smallest. The inner row is a little longer and consists of four cusps, nearly equal in size but the anterior a little the smallest. The whole inner surface of the tooth to, and perhaps beyond, the apices of the internal cusps has been sharply beveled by wear and a nearly vertical plane surface formed. The following tooth,  $P^5$ , is closely similar save that the outer cusp row is shorter, the posterior cusp being absent, and the inner slope broader, probably because of the (individual?) circumstance that this tooth is a little more external in the jaw than the preceding one.

$M^1$  is a larger and longer tooth than  $P^4$  or  $P^5$ . It differs further in the fact that it has a straight median longitudinal valley and that the cusps are higher, better separated, and have quadrate bases, rather than circular ones. The outer row has three cusps of nearly equal size and a very small anterior cuspule. The inner row has three cusps equal and opposite to those of the external row and in addition it has a well developed anterior cusp nearly as large as the others.

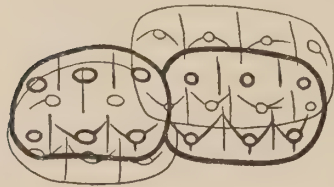


FIG. 7. *Ctenacodon*. Diagram of upper and lower molars in occlusion. Lower molar outlines darker.

$M^2$  has but two cusps in the outer row, both strongly developed, the anterior one exceptionally so. The inner cusps are three in number, without trace of another, of nearly equal size.

As was clearly shown by Marsh, the arrangement of the molars is extraordinary. The second molar is internal as well as posterior to the first, so that the outer cusp row of  $M^2$  continues the inner cusp row of  $M^1$ . The outer row of  $M^1$  and inner of  $M^2$  do not fit into the lower groove, and hence their cusps are worn only toward the midline of the respective teeth, while the inner row of  $M^1$  and

outer of  $M^2$  fit into the lower groove in occlusion and hence are reduced to mere stumps. At first sight this would appear to be an individual anomaly, but it is believed to be characteristic of the genus or, indeed, of the family. No other American specimens show both molars in place, but some show the maxilla incurved exactly as here. Exactly the same placing of the molars is seen in the closely allied English *Bolodon*. Furthermore, wear on the lower molars always seems to be such as would be brought about by such a condition in the upper molars. Finally, as will appear below, this placing of the molars offers a very apt explanation of apparent anomalies in the teeth of the *Ptilodontids*, which were presumably derived from a *plagiaulacid*-like ancestry. It is outside the present work to attempt to explain how such a novel condition can have arisen, as there is no paleontological evidence bearing directly on the matter.

## SKULL

The root of the zygoma is stout and arises opposite  $P^{3-4}$ . The arch was widely expanded and the anterior part was formed by the maxilla. The infraorbital foramen is small and is situated low down just in front of, or indeed on, the zygomatic root. Consonant with the arrangement of the molars, the posterior part of the alveolar process of the maxilla curves inward abruptly back of  $M^1$ . Much of the palate may be represented by flakes of bone, but its characters are destroyed.

## MEASUREMENTS

Lengths:

	$P^1-M^2$	$P^{1-5}$	$M^{1-2}$	$P^1$	$P^2$	$P^3$	$P^4$	$P^5$	$M^1$	$M^2$
Y.P.M. 11761	ca. 7.0	4.6	2.5	0.9	0.9	0.8	1.0	1.2	1.4	1.4
U.S.N.M. 2682	..	..	..	..	..	..	0.9	1.2	1.5	..
U.S.N.M. 2681	..	..	..	..	0.9	0.8	1.0	..	..	..

*Psalodon* Simpson 1926

1926. *Psalodon*, Simpson, *Amer. Jour. Sci.* (5) XI, 239.

DEFINITION.— $P^3$  with three cusps, but one much the largest and one vestigial.  $P^{4-5}$  more highly developed for shearing, more compressed laterally, with outer cusps reduced in number and vestigial in character. Lower jaws, doubtfully referred, close to those of *Ctenacodon* but considerably larger than any known species of the latter.

TYPE.—*Psalodon* (*Ctenacodon*) *potens* (Marsh).

DISTRIBUTION.—Morrison, Wyoming.

The circumstances which led Marsh to refer this type of upper jaw to *Ctenacodon* have been given in dealing with *Ct. laticeps*. The upper jaws here referred to *Psalodon* do differ from those referred to *Ctenacodon* sufficiently to follow Marsh in considering them as representing different genera.

If the lower jaws here referred to as ?*Psalodon marshi* do belong to *Psalodon*, they illustrate a multituberculate peculiarity which has been noticed also in dealing with later forms; that is, that the upper teeth may show very marked qualitative differences although the lower jaws at any given time may be, as it were, stereotyped, differing only in size and proportions. This has been seen in several Paleocene forms and is apparently equally true of the Cretaceous multituberculates. Ultimately the chief taxonomic characters will be found in the upper jaws, although at present associated material is too scanty to follow this method consistently.

To *Psalodon* are now referred the upper jaws on which Marsh based his *Ctenacodon potens*, the lower jaws referred to this species by Marsh, and the premaxilla called *Allodon fortis* by him. Because of the doubtful association it seems best to retain both trivial names, *potens* and *fortis*, and to refer the lower jaws to a third species, *Ps. marshi* with the understanding that these names are adopted provisionally for convenience of reference and of cataloguing and that future discoveries may prove them to be synonymous.

*Psalodon potens* (Marsh 1887)

1887. *Ctenacodon potens*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 333.

1927. *Psalodon potens*, Simpson, *Amer. Jour. Sci.* (5) XIV, 38.

TYPE.—Cat. No. 11834, Y.P.M. Right upper jaw with P<sup>1-5</sup>. Fig'd, Marsh 1887, Pl. VIII, figs. 2-3.

REFERRED SPECIMENS.—Y.P.M. No. 10363. U.S.N.M. No. 2680. Am. Mus. Nat. Hist. No. 3003. These add nothing to our knowledge of the species.

DIAGNOSIS.—Upper cheek teeth with the characters of the genus. Length P<sup>1-5</sup> ca. 8.8 mm.

## DENTITION

P<sup>1-2</sup> are essentially similar to the corresponding teeth of *Ctenacodon laticeps* save in size. They were preserved in the matrix anterior to the preserved bone and the crumbling of the matrix has dissociated them from the rest of the specimen, making it impossible to verify the original arrangement, but Marsh's figure shows them to be oriented as in *Ctenacodon* (his *Allodon*). P<sup>3</sup> differs markedly from the latter genus, however. The posterointernal cusp is very large, constituting almost the entire crown, and the anterointernal cusp is much smaller, while the external cusp is smaller still—a mere projection on the confluent slopes of the other two. It is also more anterior in position than in the preceding teeth.<sup>11</sup>

P<sup>4</sup> consists essentially of four cusps in a single row, the anterior one a little the smallest. These form a shearing edge and the internal slope is abraded. On the outer slope there are three very small and apparently quite functionless cuspules. P<sup>5</sup> is similar, with four cusps forming a sharp shearing edge, the posterior one a little the smallest. On this tooth the outer cusps are still less prominent, but a single cusp-like vestige on the anteroexternal part of the crown occurring.

## MEASUREMENTS

	Lengths:					
	P <sup>1-5</sup>	P <sup>1</sup>	P <sup>2</sup>	P <sup>3</sup>	P <sup>4</sup>	P <sup>5</sup>
Y.P.M. 11834	8.8	1.4	1.5	1.7	2.2	2.0
Y.P.M. 10363	..	1.3	..	1.7	2.1	..

*Psalodon fortis* (Marsh 1887)

1887. *Allodon fortis*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 331.

1927. *Psalodon fortis*, Simpson, *Amer. Jour. Sci.* (5) XIV, 38.

TYPE.—Cat. No. 11760, Y.P.M. Right premaxilla with I<sup>2-3</sup> and alveolus for I<sup>1</sup>. Fig'd, Marsh 1887, Pl. VII, figs. 7-10.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

<sup>11</sup> The apparent fourth cusp posterior to the main one in Marsh's woodcut is merely a shoulder on the largest cusp and not a distinct projection.



DIAGNOSIS.—A large premaxilla probably belonging to *Psalodon potens* and not directly comparable with any other American material. Differs from *Bolodon* especially in the simple  $I^3$ , resembling  $I^2$  save in size.

## DENTITION

$I^1$  was very small, closely appressed to the equivalent tooth of the opposite side, and directed more forward than downward.  $I^2$ , on the contrary, is much enlarged. The root is long and large, but must have been closed in the adult as the crown is definitely delimited and is not very long. The tooth is inclined at about  $60^\circ$  from the horizontal. The anterior and lateral faces of the crown are not distinguished from one another and are convex, with faint longitudinal flutings. The median face is nearly plane and was apparently in contact with  $I^2$  of the opposite side. This face is separated from the posterolateral face by a marked angulation, on which the wear chiefly occurs. Above the facet of wear and slightly external to it is a small accessory cusp. The posterolateral face is small, lies below this cusp, and is distinctly concave.

$I^3$  is about half as large as  $I^2$  and nearly parallel to it. The tip is rounded, subspatulate, and there is a very small accessory cusp. There is evidence of wear similar to that on  $I^2$ . The lower incisors probably could work against either  $I^2$  or  $I^3$  at will.

## SKULL

The nares open terminally just above the anterior incisors and are small. The anterior palatine foramen is large and is at the extreme anterior end of the palate just internal to  $I^3$ . The premaxilla is a triangular bone of moderate size. Its suture with the maxilla, in the lower part at least, is very steep.

*?Psalodon marshi*, new species

TYPE.—U.S.N.M. No. 2684. Crushed and broken left lower jaw with the incisor,  $P_{1-4}$ , and  $M_1$ . Fig'd, Marsh 1887, Pl. VIII, figs. 7-9.

PRINCIPAL REFERRED SPECIMENS.—U.S.N.M. No. 2687. Broken lower jaw with  $I$ ,  $P_{2-4}$ , and  $M_1$ .

U.S.N.M. 2690.  $P_{2-4}$ .

Y.P.M. No. 13669. Isolated  $P_4$ .

U.S.N.M. 2679. Isolated broken lower incisor. Fig'd, Marsh 1887, Pl. VII, figs. 14-15.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Lower jaws and teeth possibly belonging to *Psalodon potens*. Length  $P_{1-4}$ , *ca.* 6.5 mm.

In addition to its larger size, Marsh considered the lower  $M_2$  and more perpendicular coronoid as distinguishing these jaws from *Ctenacodon serratus*. The size alone is sufficient to indicate such specific distinction, but the other characters cited by Marsh appear to be due to crushing. It is not possible at present to point to any generic distinctions between *?Psalodon marshi* and *Ctenacodon serratus*, but it is more than

possible that such would be visible were better material at hand. The incisor, for instance, is unknown in American *Ctenacodon* lower jaws, and later multituberculates show that differences in the incisors may in some cases be the only outstanding generic characters in lower jaws. As already explained, *Psalodon* is based on an upper jaw, and ?*Ps. marshi* is doubtfully referred to the genus because it includes the only known lower jaws which could belong here and because it is larger than any upper or lower jaws referred to *Ctenacodon*.

#### DENTITION

The lower dental formula is that of *Ctenacodon*. The incisor is a large, sharply pointed tooth, flattened on the inner side. Its root extends back beneath the first molar. The premolars differ somewhat in proportions, but are morphologically similar to those of *Ctenacodon*, so far as displayed, and require no separate description. The isolated  $P_4$  (Y.P.M. No. 13669) is almost unworn and gives the characters of this unusual tooth more clearly than any other known specimen pertaining to the Plagiaulacidae. The oblique lateral ridges are seen to be better developed than would be gathered from worn material, being about as long as in the English *Ctenacodon* (*Plagiaulax*) *minor* (Falconer). Along the base of the outer face is a row of small accessory cusps. Beginning at the posterior end of the tooth, there is a single blunt protuberance, then a space with faint indications of a cusp, then four cusps becoming progressively larger. The most anterior cuspule is at a point about one-third of the length of the tooth from its anterior edge. The line along which these cuspules is arranged is oblique with respect to the crown, but was horizontal in the correct orientation of the jaw. These projections are already truncated on this almost unworn tooth and are nearly or quite removed by wear in all the other American specimens, although clearly seen in some from England. This speedy obliteration after the tooth came into use explains the fact that previous investigators have overlooked this unusual, but minor, character. The anterior end of  $P_4$  bears a triangular depression into which the posterior end of  $P_3$  fitted.

The first molar is preserved on two specimens, but so much worn that nothing further can be ascertained than that it had six cusps as in *Ctenacodon*.

#### MANDIBLE

The mandible is not well shown. It apparently was much stouter than in *Ctenacodon*.

#### MEASUREMENTS

Measurements of the type in millimeters.

Lengths:

$P_1-M_2$	$P_{1-4}$	$P_1$	$P_2$	$P_3$	$P_4$	$M_1$	$M_2$
ca. 10.7	ca. 6.5	0.7	1.7	1.7	3.0	2.1	ca. 2.1

## ORDER TRICONODONTA Osborn

DEFINITION.—Incisors small and three or four in number. Canines present. Molars always with three main cusps arranged in a longitudinal series, the central cusp of the lower molars somewhat higher than the other two and the anterior and posterior cusps subequal. Internal cingulum present. Lower molars shearing obliquely up the internal slope of the upper molars. Mandible without angular process, with distinct masseteric and pterygoid crests and high strong coronoid. Zygomata stout, not expanded laterally, arising from posterior ends of alveolar processes of maxillae.

DISTRIBUTION.—Middle and upper Jurassic, England. Upper Jurassic, North America.

The triconodonts are confined to the Jurassic, but here play an important part. They are the carnivorous mammals of the period and are relatively abundant in each of the three best known Jurassic mammalian faunas. One of the two Mesozoic mammals first brought to scientific attention was a triconodont. At first confused with *Amphitherium*, a pantothere, it was placed in a distinct genus, *Phascolotherium* by Owen in 1838. The essential unity of the group was clearly recognized by Owen, who in 1871 placed *Phascolotherium*, *Triacanthodon*, and *Triconodon* together. In 1887 Marsh proposed and accurately defined the family Triconodontidae, to include *Triconodon*, *Priacodon*, and possibly some other genera not specified. Marsh, however, did not clearly differentiate between triconodonts and symmetrodonts, a confusion which has been shared by most subsequent writers. Thus he at first referred a typical triconodont, *Priacodon ferox*, to the symmetrodont genus *Tinodon*. This mistake he soon corrected, but in 1887 he still referred the triconodont *Phascolotherium* to the family Tinodontidae, although with doubt.

There is some question whether Marsh intended to include the Triconodontidae in his order Pantotheria. He nowhere made a clear statement on this point, but there is some reason to believe that he did not. Thus (1887, p. 345) he says in defining the Pantotheria "Premolars and molars imperfectly differentiated" while of the Triconodontidae he says (p. 341) "In this group the premolars are unlike the molars." He also states that the pantotherian angle is without inflection, whereas it was then universally believed that the triconodont angle was inflected. It is clear that the order Pantotheria was not defined with the triconodonts in mind, and it is probable that he meant to leave the latter *incertae sedis*, for they are obviously excluded from the Allotheria also.

Osborn (1888A) at first referred the triconodonts to his "Prodidelphia" along with the Amphitheriidae, Peralestidae, and Kurtodontidae. He enlarged the family Triconodontidae, including three subfamilies. The subfamily Amphilestinae was Marsh's Triconodontidae with the addition of *Amphilestes*, which Marsh had not mentioned, and of *Amphitylus*, a form which, as Osborn later recognized, belongs in a different order. Osborn's Phascolotheriinae of 1888 was identical with Marsh's Tinodontidae, including *Phascolotherium* and *Tinodon*, and his Spalacotheriinae was Marsh's Spalacotheridae, including *Spalacotherium* and *Menacodon*. The term Tri-



conodonta was first used by Osborn in this memoir (1888A, p. 251) being there applied to a hypothetical group supposed to be ancestral to the triconodonts proper and to certain other mammals (*Asthenodon*, *Stylacodon*). In a succeeding paper published the same year (1888B), Osborn more definitely recognized the presence in the Jurassic of two molar types (in addition to the multituberculate), which he called triconodont and trituberculate. The word "triconodont" hence passed into vernacular usage as a morphological term and, by extension, as a name for any mammal belonging to the group with triconodont molars. Its first use for a definite taxonomic division was apparently in Zittel's *Handbuch* (1893, p. 97) where "Triconodonta Osborn" is made a group under the suborder Polyprotodontia.

In 1907 (p. 21) Osborn elevated the group to ordinal rank. Only one family is recognized, as before, but under Amphilestinae is only *Amphilestes*, while *Triconodon*, *Triacanthodon*, and *Priacodon* form the subfamily Triconodontinae. The Phascolotheriinae are as before, and the Spalacotheriinae (to which *Peralesstes* is added) are considered as *incertae sedis*.

Subsequent work has been chiefly based on the literature only and has been largely devoted to the question whether all the genera referred by Osborn to the order belong there. Thus Gregory (1910, p. 173) at first decided that *Amphilestes*, *Phascolotherium*, *Triconodon*, and *Priacodon* certainly were related and that the other genera (our symmetrodonts) probably were correctly referred here. Matthew, however (in Gregory 1922, p. xiii), concluded that *Spalacotherium* and its allies had nothing to do with the true triconodonts.

Finally, the present writer has already proposed a new classification of the order (1925B, p. 357) which differs from Osborn's chiefly in removing the allies of *Spalacotherium* and in placing *Phascolotherium* in the Amphilestinae rather than in a distinct subfamily. With a generic change to be explained below, this classification has been supported by subsequent work. A complete arrangement in the light of recent studies is here given:

## CLASS MAMMALIA Linnaeus 1758

*Incertae sedis*:

### ORDER TRICONODONTA Osborn (1888)

Family Triconodontidae Marsh 1887

Subfamily Amphilestinae Osborn 1888

*Amphilestes* Owen 1859

*Phascolotherium* Owen 1838

*Phascolodon* Simpson 1925

*Aploconodon* Simpson 1925

Subfamily Triconodontinae Osborn 1907

*Triconodon* Owen 1859

*Trioracodon* Simpson 1928

*Priacodon* Marsh 1887

The morphology of the American Triconodonts has already been treated (Simpson 1925B), and it is not proposed to repeat the details here. Formal definitions are

here given, however, with some changes made possible by study of European material and with such data as are necessary to maintain the continuity of this memoir.

### TRICONODONTIDAE Marsh 1887

DEFINITION.—(With the characters of the order.)

TYPE.—*Triconodon* Owen.

DISTRIBUTION.—As for the order.

### AMPHILESTINAE Osborn 1888

DEFINITION.—Premolars symmetrical and submolariform. Molars more than four in number, with the anterior and posterior cusps small relative to the main cusp.

TYPE.—*Amphilestes* Owen.

DISTRIBUTION.—Stonesfield slate of England and (?) Morrison formation of Wyoming.

This primitive subfamily is represented in England by *Amphilestes* and *Phascolotherium* from the middle Jurassic Stonesfield slate. One of the most unexpected results of the present work was the discovery in the Marsh Collection in the United States National Museum of two new genera which can only be placed here, although they are of uppermost Jurassic age and contemporaneous with the more highly developed triconodontines. These genera, which have been named *Phascolodon* and *Aploconodon*, are very poorly known and their position in the system may possibly be changed by the discovery of better material.

#### *Phascolodon* Simpson 1925

1925. *Phascolodon*, Simpson, *Amer. Jour. Sci.* (5) X, 334.

DEFINITION.—Molars probably more than four. Accessory cusps about half the height of the main cusp, the latter rather blunt, and gibbous externally. Internal cingulum curving upward slightly in the middle and rising to form small anterior and posterior cingulum cusps at the ends. Last molar much reduced in size, similar to preceding tooth but without cingulum cusps.

TYPE.—*P. gidleyi* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

The molars of this genus are strikingly like those of *Phascolotherium*, but it can readily be distinguished by the smooth enamel, by the character of the cingulum, and by the reduction of the last molar.

#### *Phascolodon gidleyi* Simpson 1925

1925. *P. gidleyi*, Simpson, *Amer. Jour. Sci.* (5) X, 334.

TYPE.—U.S.N.M. No. 2703. Fragments of left lower jaw, with the last four molars.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Lengths of last three molars: 1.6, 1.2, and 0.7 mm. respectively.

*Aploconodon* Simpson 1925

1925. *Aploconodon*, Simpson, *Amer. Jour. Sci.* (5) X, 336.

DEFINITION.—(Number of molars unknown.) Accessory cusps very minute, less than half height of main cusp, the latter more acute and slender than in *Phascolodon*.

Molar cingulum obsolete in middle and forming no cingulum cusps. Last molar much reduced in size, with relatively higher accessory cusps than on the preceding tooth.

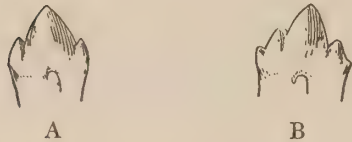


FIG. 8. Morrison Amphilestinae. External views of penultimate lower molars. A, *Aploconodon comoënsis*. B, *Phascolodon gideleyi*. A, ten times natural size. B, eleven times natural size. (After Simpson, 1925B.)

TYPE.—*A. comoënsis* Simpson.

DISTRIBUTION.—Morrison formation of Wyoming.

Although very poorly known, this extraordinary genus is very distinctive. It is the only known triconodont in which cingulum cusps are missing on the penultimate molar, and on this same tooth the accessory cusps are smaller than in any other known genus of the

group. This tooth is suggestive of the premolars of the Stonesfield triconodonts and it is either a remarkable example of the survival of a primitive type or a still more remarkable example of secondary simplification. The presence of the last molar in the only known specimen fortunately removes all doubt as to identification.

*Aploconodon comoënsis* Simpson 1925

1925. *A. comoënsis*, Simpson, *Amer. Jour. Sci.* (5) X, 336.



FIG. 9. Cynodonts and triconodonts. Internal views of lower molars. A, *Ictidopsis*. B, *Microconodon*. C, *Amphilestes*. D, *Phascolotherium*. E, *Priacodon*. F, *Triconodon*. Not to scale.

TYPE.—U.S.N.M. No. 2791. Fragment of right lower jaw with last two molars.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Lengths of last two molars: 1.1 and 0.7 mm. respectively.

TRICONODONTINAE Osborn 1907

DEFINITION.—Premolars asymmetrical, more or less recurved, the last ones higher than the first molars. Molars four or three in number, with anterior and posterior cusps nearly or quite equal to the midcusp.



TYPE.—*Triconodon* Owen.

DISTRIBUTION.—Purbeck beds of England and Morrison formation of Wyoming.

*Trioracodon* Simpson 1928

1928. *Trioracodon*, Simpson, *Cat. Mes. Mam. Brit. Mus.*, 88.

DEFINITION.—Dental formula  $I_1^1 C_1^1 P_4^4 M_3^3$ . Anterior and posterior cusps of lower molars a little lower relative to the midcusp than in *Triconodon*. Cheek tooth series closed, molars relatively large.  $M^3$  reduced and bicuspid.

TYPE.—*Trioracodon ferox* (Owen).

DISTRIBUTION.—Purbeck beds of England and Morrison formation of Wyoming.

Marsh supposed (1887) that there were three upper Jurassic genera of triconodonts, distributed as follows:

Purbeck	Morrison
<i>Triacanthodon</i>	
<i>Triconodon</i> . . . . .	<i>Triconodon</i>
	<i>Priacodon</i>

The dental formulae were supposed to be:

<i>Triconodon</i> : $P_4 M_3$
<i>Triacanthodon</i> : $P_4 M_4$
<i>Priacodon</i> : $P_3 M_4$

The first two formulae were assigned by Owen, the last by Marsh. Osborn (1888A) questioned this arrangement and gave reasons for believing that *Triacanthodon* is a synonym of *Triconodon* and that this genus had the formula  $P_4 M_4$ . The writer (1925B) showed that in the American species referred by Marsh to *Triconodon* there were never more than three molars, and largely on this basis he continued to maintain the separate status of *Triacanthodon*. This view is now acknowledged to have been erroneous. Study of the original English material has shown beyond question that Osborn was right in considering *Triconodon* and *Triacanthodon* as synonymous and in assigning to *Triconodon* the formula  $P_4 M_4$ . It has further been found, however (see Simpson 1928B, p. 88 seq., for details), that there does occur in the Purbeckian an allied genus with a formula of  $P_4 M_3$  and with various other differences from *Triconodon*, to which the name *Trioracodon* has been applied. The American species "*Triconodon*" *bisulcus* belongs to this genus, being especially close to the Purbeckian *Trioracodon oweni* Simpson. The result of this change is that the application of the various names is modified but that the essential facts remain the same as supposed by Marsh, as may be seen in the following tabular presentation:

Purbeck	Morrison	Cheek Teeth
<i>Triconodon</i>		$P_4 M_4$
<i>Trioracodon</i> . . . . .	<i>Trioracodon</i>	$P_4 M_3$
	<i>Priacodon</i>	$P_3 M_4$

It may be emphasized that these formulae have been checked wherever necessary by actual dissection of the jaws, to make certain that no successional or posterior unerupted teeth remained uncounted, and that the separation of the genera does not rest solely on the dental formulae.

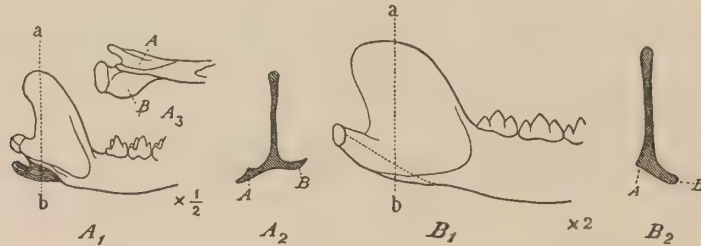


FIG. 10. A<sub>1</sub>. Posterior portion of right lower jaw of *Dasyurus maculatus* (Y.P.M.O. No. 253) from the outside.

A<sub>2</sub>. Section of same along line a-b. A, Inflected ridge running forward from the angle. B, Flange bordering the masseteric fossa inferiorly.

A<sub>3</sub>. The same jaw from above.

B<sub>1</sub>. Posterior portion of the right lower jaw of *Trioracodon bisulcus* (restored), from the outside. The oblique dotted line indicates the course of the pterygoid ridge on the inner side of the mandible.

B<sub>2</sub>. Section of same along line a-b. A, Pterygoid ridge, sometimes considered homologous with the angle of *Dasyurus*. B, Flange below the masseteric fossa. (After Simpson, 1925B.)

### *Trioracodon bisulcus* (Marsh 1880)

1880. *Triconodon bisulcus*, Marsh, *Amer. Jour. Sci.* (3) XX, 237.

1928. *Trioracodon bisulcus*, Simpson, *Cat. Mes. Mam. Brit. Mus.*, 76.

TYPE.—Y.P.M. No. 11851. Part of right lower jaw with broken P<sub>4</sub> and M<sub>1-3</sub>.

REFERRED SPECIMENS.—Various jaws, both upper and lower. See Simpson 1925B.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—M<sub>3</sub> markedly shorter than M<sub>2</sub>. Length M<sub>2</sub> about 3.1 mm. Molar cusps relatively slender, with straight anterior and posterior contours. Depth of jaw below anterior end of M<sub>3</sub>, 4.0-4.4 mm.

### *Priacodon* Marsh 1887

1887. *Priacodon*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 341.

DEFINITION.—Dental formula I<sup>3</sup> C<sub>1</sub><sup>1</sup> P<sub>3</sub><sup>3</sup> M<sub>4</sub><sup>4</sup>. Anterior and posterior molar cusps a little lower relative to the midcusp than in *Triconodon*. Diastemata following the canines. M<sup>8</sup> unreduced, tricuspid. M<sup>4</sup> bicuspid.

TYPE.—*Priacodon ferox* (Marsh).

DISTRIBUTION.—Morrison formation, Wyoming.

Osborn (1888A, p. 229) questioned the right of this form to generic separation from *Triconodon*. He suggested that the type (of *Priacodon ferox*) might be immature, with a deciduous tooth in place. The present writer (Simpson 1925B, p. 160) concluded that this was not the case. These findings have since been carefully

compared with those from the pertinent European material and are fully confirmed. From these comparisons, from the several lower jaws now referred to *Priacodon*, and from the upper jaws which clearly have three premolars and four molars, there can be little doubt that the definitive formula of *Priacodon* is  $P_3^3 M_4^4$  and that the genus is distinct from either *Triconodon* or *Trioracodon*, although closely related to both.

#### *Priacodon ferox* (Marsh 1880)

1880. *Tinodon ferox*, Marsh, *Amer. Jour. Sci.* (3) XX, 236.

1887. *Priacodon ferox*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 341.

1888. *Priacodon* (*Triconodon?*) *ferox*, Osborn, *Jour. Acad. Nat. Sci. Phila.*, IX, 229.

1898. *Triconodon ferox* Owen, Trouessart, *Cat. Mam.*, 1250. (Error.)

TYPE.—Y.P.M. No. 606. Right lower jaw in matrix, inner aspect, with  $P_{1-3}$ ,  $M_{1-3}$  and alveoli for other teeth.

REFERRED SPECIMEN.—Y.P.M. No. 13626. Right maxilla, nearly complete, with crowns of  $M_{1-3}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.— $M_3$  longer than  $M_2$  and with strong posterior cingulum cusp.  $P_1 = P_2$ .  $P_2$  with no anterior cusp, low central cusp, faint cingulum. In upper jaw (referred), lengths of first three molars about 2.0, 2.6, and 2.7 respectively; a broad palatal groove internal to raised molar border; upper molars with sharp continu-

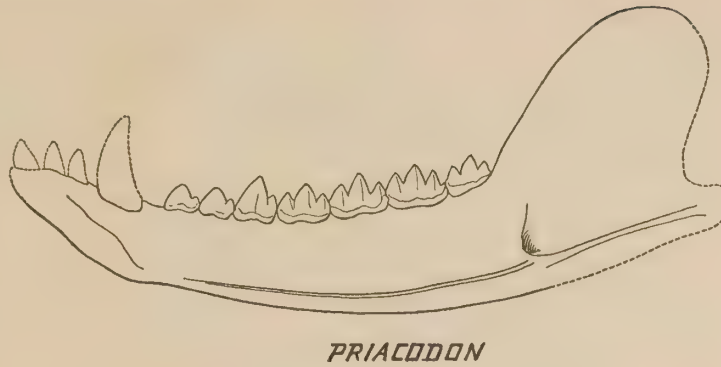


FIG. 11. *Priacodon*. Diagrammatic internal view of right lower jaw. Three times natural size.

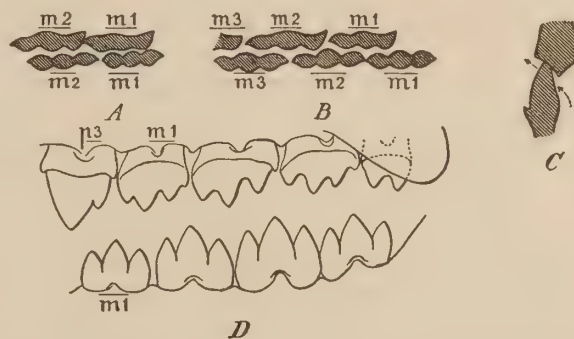


FIG. 12. Occlusion in triconodonts. A. On the hypothesis that cusp *b* below occludes between *a* and *b* above. B. The correct relationships, with *b* below fitting between the teeth above. C. Section through the center of a lower cusp in occlusion, showing how the tip scrapes upward and inward while shearing against the upper molar. D. Somewhat schematic view of left molar series from the outside, showing the relationships of the cusps of the lower molars to the notches in the crests of the upper molars. (After Simpson, 1925B.)



ous external cingulum and with internal cingular cusps; anterior border of orbit above  $M_1$ .

The occasional reference of this species to *Triconodon* has led to its being sometimes confused with *Triconodon ferox* (now *Trioracodon ferox*) Owen, with which it has nothing to do.

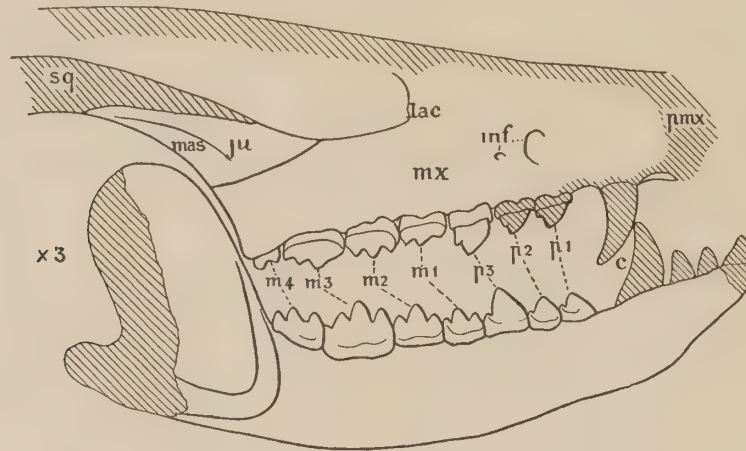


FIG. 13. Skull and jaws of *Priacodon*, seen from the right side. The cross-lined portions are restored. The restoration is composite, although largely based on specimens of *Priacodon ferox*. Inf, Infra-orbital foramina; ju, Jugal; lac, lacrymal notch; the foramen is just internal to this point; mas, origin for the masseter muscle; mx, maxilla; pmx, premaxilla; sq, squamosal. (After Simpson, 1925B.)

### *Priacodon robustus* (Marsh 1879)

1879. *Tinodon robustus*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 397.

1925. *Priacodon robustus*, Simpson, *Amer. Jour. Sci.* (5) X, 162.

TYPE.—Y.P.M. No. 11846. Part of left lower jaw with  $P_3$  and  $M_{1-3}$ .

REFERRED SPECIMEN.—Y.P.M. No. 10343. Part of left lower jaw with  $P_{2-3}$  and  $M_1$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.— $M_3$  about equal to  $M_2$  and with posterior cingulum cusp small.  $P_1$  shorter than  $P_2$ .  $P_2$  with small anterior cusp, high central cusp, and sharp cingulum. Upper teeth unknown.

### *Priacodon lulli* Simpson 1925

1925. *P. lulli*, Simpson, *Amer. Jour. Sci.* (5) X, 346.

TYPE.—Y.P.M. No. 13625. Part of right maxilla, with  $P^3$  and  $M^{1-4}$ .

REFERRED SPECIMEN.—Y.P.M. No. 10359. Part of right maxilla with  $M^{1-2}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Grooves of wear on upper molars such as to prevent occlusion with lower molars of *P. robustus*. Lengths of first three upper molars about 2.3, 3.0, and 2.5 mm. respectively. Broad palatal groove internal to raised molar border. External molar cingula continuous but faint. No internal cingular cusps. Bases of upper molars gibbous. Anterior border of orbit above last pre-molar.

*Priacodon grandaevus*

Simpson 1925

1925. *P. grandaevus*, Simpson, *Amer. Jour. Sci.* (5) X, 350.

TYPE.—Y.P.M. No. 10349.

Part of left maxilla with M<sup>1-3</sup>.

REFERRED SPECIMEN.—U.S.N.M. No. 2698. Part of right maxilla with M<sup>1-3</sup>.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Grooves of wear on upper molars such as to prevent occlusion with lower molars of *P. robustus*. Lengths of first three upper molars about 2.1, 2.3, and 2.4 mm. respectively. Molar border little raised. No palatal groove. External upper molar cingula sharp, continuous. Internal cingular cusps present.

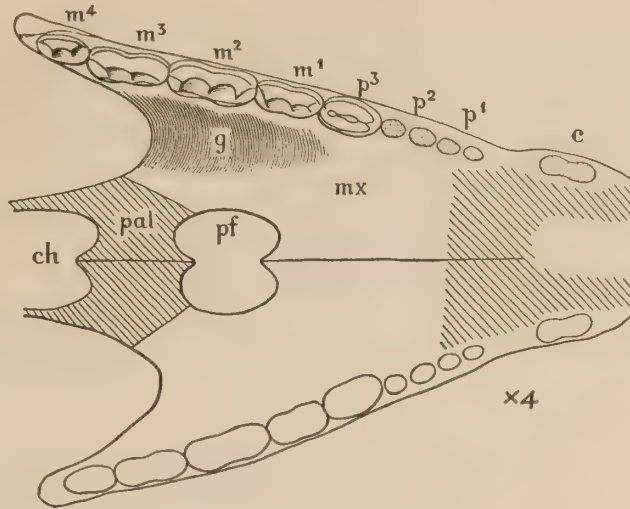


FIG. 14. Palate of *Priacodon*, seen from below. The cross-lined portions are restored. Ch, internal nares; g, broad groove internal to raised alveolar border (not seen in all species of *Priacodon*); mx, palatal process of maxilla; pal, palatal process of palatine; pf, palatal vacuity. (After Simpson, 1925B.)

## ORDER SYMMETRODONTA Simpson

DEFINITION.—Lower molars nearly or quite symmetrical with respect to a transverse median plane, with a high centroexternal cusp, lesser anterior and posterior internal cusps, and a well developed internal cingulum below the latter. No true heel or talonid. Upper molars with a high centroiinternal cusp, anterior and posterior external cusps on its slopes, and an external but no internal cingulum. Incisors not enlarged, canines present. Mandible with slight pterygoid crest but no angular process.

DISTRIBUTION.—Upper Jurassic of England and the United States.

One of the greatest recent advances in the interpretation of Jurassic mammals is the perception, first by Matthew (in Gregory 1922, p. xiii), of the fact that the forms which the writer calls symmetrodonts have no intimate relationship with the triconodonts. As already pointed out in dealing with the latter group, almost all classifica-

tions since Owen have agreed in considering the symmetrodonts and triconodonts as very closely related. The taxonomic history of the group need not be repeated here.

Provided that the essential unity of the group and its fundamental differences from the Triconodonta and somewhat less fundamental but still very important differences from the Pantotheria are recognized, it is of relatively little importance whether it is given ordinal rank or less. Subordinal position under the Pantotheria might be equally justified, although the supposed transitional steps to the true pantotheres do not exist and any actual link between the two groups is as yet unknown.

Like the triconodonts, the symmetrodonts have recently been treated in detail by the author (1925c, and 1928B), so that formal definitions with such slight changes as further study has indicated will here suffice. The following classification is proposed:

- CLASS MAMMALIA Linnaeus 1758
  - SUBCLASS THERIA Parker & Haswell
    - ORDER SYMMETRODONTA Simpson 1925
      - Family Spalacotheriidae Marsh 1887
        - Spalacotherium* Owen 1854
        - Peralestes* Owen 1871
        - Tinodon* Marsh 1879
      - Family Amphidontidae Simpson 1925
        - Amphidon* Simpson 1925
      - Incertae sedis:*
        - Eurylambda* Simpson, new genus.

Both families and the last three genera occur in the American Morrison formation.

### SPALACOTHERIIDAE Marsh 1887

DEFINITION.—Lower molars functionally tricuspid. Antero- and posterointernal cusps distinct and well developed, springing from base of crown. Internal cingulum continuous, rising to form small anterior and posterior cingulum cusps.

TYPE.—*Spalacotherium* Owen.

DISTRIBUTION.—Upper Jurassic of England and the United States.

#### *Tinodon* Marsh 1879

1879. *Tinodon*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 216.

1887. *Menacodon*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 340.

DEFINITION.—Dental formula  $I_1 C_1 P_3 M_4$ . Molars longer than high, no external cingulum. Premolars symmetrical, not recurved. Coronoid arising at an angle of about  $90^\circ$  to the alveolar border.

TYPE.—*Tinodon bellus* Marsh

DISTRIBUTION.—Upper Jurassic, Wyoming.



*Tinodon* and *Menacodon* were referred by Marsh to different families, by Osborn to distinct subfamilies, but they prove to be synonymous. Marsh did not directly compare them, and reëxamination shows conclusively that the apparent distinctions are due solely to slight differences in preservation. Only two species can now be recognized, and these are doubtfully distinct.

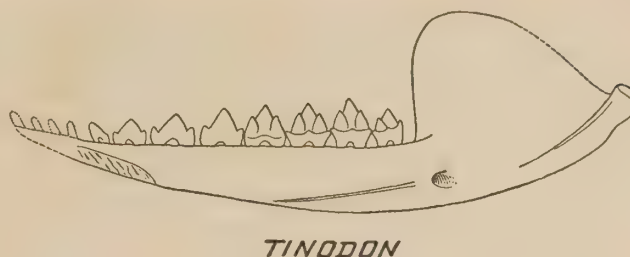


FIG. 15. *Tinodon*. Diagrammatic internal view of right lower jaw. Three times natural size.

### *Tinodon bellus* Marsh 1879

1879. *T. bellus*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 216.

TYPE.—Y.P.M. No. 11843. Right lower jaw in matrix, inner aspect, with  $M_{1-4}$ .

REFERRED SPECIMEN.—Y.P.M. No. 13644. Left lower jaw in matrix, inner aspect, with  $P_{1-3}$  and  $M_{1-4}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.— $M_1$  with rounded relief, faint cingulum, no trenchant edge on main cusp.  $M_{2-3}$  with relatively broad cingula.

The above diagnosis separates the species from *T. lepidus*, but it is very probable that these differences are due solely to wear or to state of preservation.

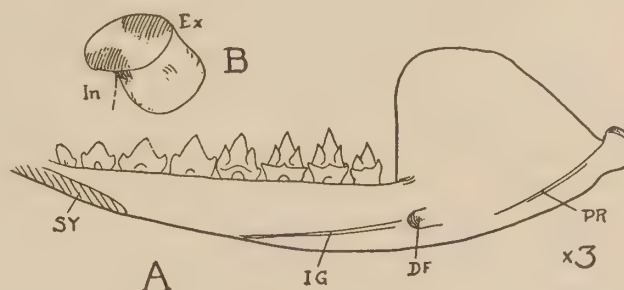


FIG. 16. *Tinodon bellus* Marsh. A, outline restoration of mandible, internal aspect,  $\times 3$ . DF, dental foramen; IG, internal groove; PR, pterygoid ridge; SY, symphysis. B, posterior view of condyle, much enlarged. Ex: external side. In: internal side. (After Simpson, 1925c.)

### *Tinodon lepidus* Marsh 1879

1879. *T. lepidus*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 398.

1887. *Menacodon rarus*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 340.

TYPE.—Y.P.M. No. 11845. Part of left lower jaw in matrix, inner aspect, with broken  $M_1$  and  $M_3$ .

TYPE OF *MENACODON RARUS*.—U.S.N.M. No. 2131. Part of left lower jaw with C,  $P_{1-3}$  and  $M_{1-3}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.— $M_1$  with sharp relief, sharp cingulum, trenchant edges on main cusp.  $M_{2-3}$  with somewhat narrower cingula.

Marsh based this species on (1) its supposedly smaller teeth, (2) the inflected inner margin with angle extending down below condyle, and (3) the lack of elevation of the condyle above the level of the alveolar border. The first character must have been cited inadvertently, for Marsh's own measurements show that the teeth are of exactly the same size as in *T. bellus*. The second and third characters are due entirely to the broken and crushed nature of the specimen and to the difficulty of orienting it. The only differences of any importance from *T. bellus* are those given in the diagnosis, and it is by no means certain that these are not due to some cause other than real specific distinction. In Marsh's descriptions of *Menacodon* and *Tinodon* the only directly comparable character is the relative vagueness of the internal groove in the former. This is not of specific or greater value, and there can be no doubt that *Menacodon rarus* is synonymous with *Tinodon lepidus*.

### AMPHIDONTIDAE Simpson 1925

DEFINITION.—Lower molars functionally unicuspid. Accessory cuspules mere crenulations in sharp cutting edges of main cusp. No continuous cingulum, but anterior and posterior inner basal projections, which may form small cusps.

TYPE.—*Amphidon* Simpson.

DISTRIBUTION.—Upper Jurassic of Wyoming.

This family rests on a single specimen, but the characters of this specimen are so clearly displayed and so extraordinary that its right to this distinction can hardly be questioned. Teeth resembling these molars, even by convergence, are not known in any other animal, living or extinct. The reference of the Amphidontidae to the Symmetrodonta is not certain, but it seems probable. The mandible, so far as known, seems to be of symmetrodont type, the premolars are similar, and the molars, while very different in detail from those of *Spalacotherium* or *Tinodon*, seem to have a certain basic resemblance. Certainly there is no other order as yet established to which the Amphidontidae could be reasonably referred.

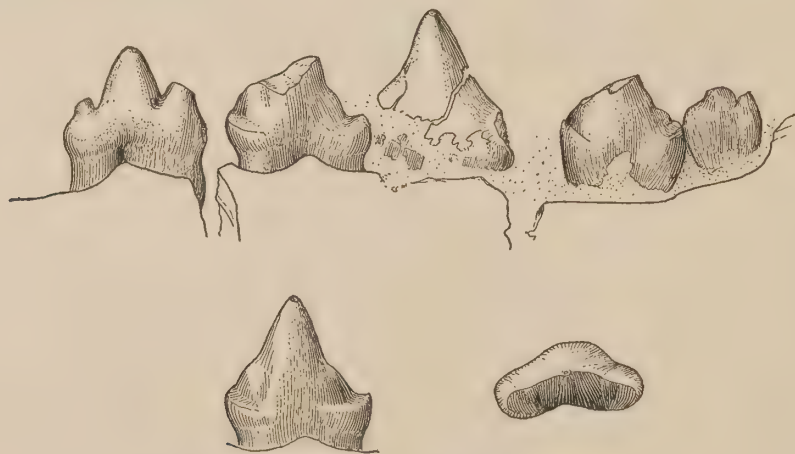


FIG. 17. *Amphidon superstes*. Above, right last premolar and molars, internal view, type. Below, restoration of  $M_1$ , internal and crown views. Fifteen times natural size.

*Amphidon* Simpson 1925

1925. *Amphidon*, Simpson, *Amer. Jour. Sci.* (5) X, 460.

DEFINITION.—Sole known genus certainly referable to the family. Dental formula  $I, C_1 P_4 M_4$ .

TYPE.—*A. superstes* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

*Amphidon superstes* Simpson 1925

1925. *A. superstes*, Simpson, *Amer. Jour. Sci.* (5) X, 460.

TYPE.—Y.P.M. No. 13638. Part of right lower jaw, with  $P_4$  and  $M_{1-4}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole known species of the genus. Lengths of molars 1 to 4, 1.3, 1.2, 1.1, and 0.7 mm. respectively.

Incertae sedis

*Eurylambda*, new genus

DEFINITION.—Upper molars triangular, about twice as long as wide, with high centrointernal main cusp. Antero- and posterointernal shearing edges, the former with one and the latter with two small cusps. Molar somewhat basined externally, with a raised external cingulum. No internal cingulum.

TYPE.—*Eurylambda* ("*Amphidon*") *aequicrurius* (Simpson).

DISTRIBUTION.—Morrison formation, Wyoming.

This is the only upper molar type in the American Mesozoic referable with any probability to the Symmetrodonta and it also represents a type of upper molar new among the Mammalia. It is therefore essential that it should bear a distinctive name. In 1925 the writer referred it provisionally to *Amphidon*, although noting that it would require a somewhat shorter lower molar than those of the genotype and suggesting possible relationship to *Tinodon*. (Simpson, 1925c, p. 464.) At the same time the resemblance to the English *Peralesstes* was emphasized and it was considered possible that *Peralesstes* represented the upper dentition of an otherwise unknown amphidotid. Since that date, however, the originals of *Peralesstes* have been studied and it has been found that the latter is with-

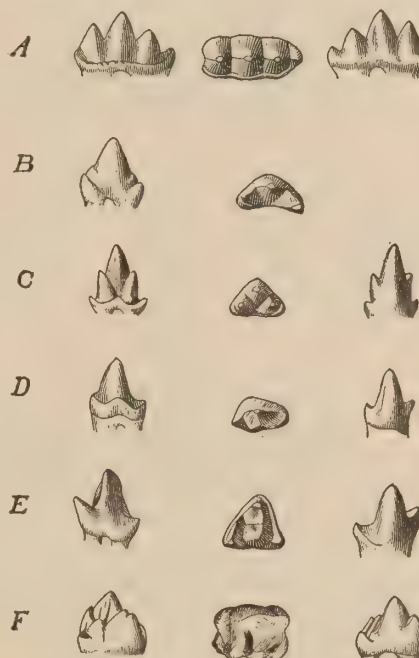


FIG. 18. Morrison mammals. Internal, crown, and external views of typical right lower molars. A, *Priacodon*. B, *Amphidon*. C, *Tinodon*. D, *Paurodon*. E, *Dryolestes*. F, *Docodon*. Not to scale.



out doubt a spalacotheriid and probably the upper dentition of *Spalacotherium* itself. This makes it possible or even probable that the present upper jaw also belongs to the Spalacotheriidae rather than to the Amphidontidae. Reference to *Tinodon* would be possible, but in view of the very doubtful character of the evidence and of the lack of association it seems less misleading to give a new generic name, *Eurylembda*, to "*Amphidon*" *aequicrurius*.

*Eurylembda aequicrurius* (Simpson 1925)

1925. *Amphidon aequicrurius*, Simpson, *Amer. Jour. Sci.* (5) X, 463.

TYPE.—Y.P.M. No. 13639. Part of right maxilla with one molar.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Length of known molar 2.0 mm.

## ORDER PANTOTHERIA Marsh

DEFINITION.—Incisors not specialized. Canines present, often bifanged. Premolars generally piercing and trenchant, never fully molariform and usually quite unlike the molars. Molars primitively trigonal, interlocking, and always to some extent overlapping in occlusion. The upper molars with

one main inner cusp and one main outer cusp (which may be much reduced) and always two or more other cusps variously developed. The lower molars with an asymmetrical trigonid of three cusps (or rarely more) and a talonid which is primitively unbasined and with a single cusp but in the most specialized family (Docodontidae) is basined and with more than one cusp. Lower molars sometimes with an outer, but never with an inner, cingulum. Primitive cheek tooth formula apparently  $P_4^4 M_8^8$ , but may be considerably reduced. Mandible not ankylosed at symphysis, with distinct coronoid, condylar, and angular processes. Angle not inflected.

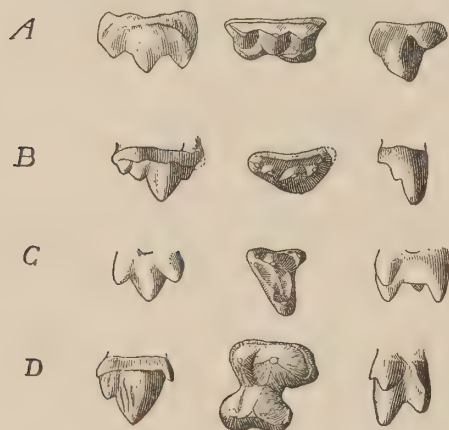


FIG. 19. Morrison mammals. External, crown, and anterior views of typical right upper molars. A, *Priacodon*. B, *Eurylembda*. C, *Melanodon*. D, *Docodon*. Not to scale.

DISTRIBUTION.—Middle Jurassic, England. Upper Jurassic, England, United States, East Africa.

This is the most abundant, most varied, and, from a phylogenetic point of view, most important of the Jurassic orders of mammals. In view of the extent to which the other Jurassic mammals, although very unlike any of the Tertiary or recent orders, have been subordinated to the latter in the usual classifications, it is not surprising to

find this distortion of perspective acting even more strongly in the usual treatment of the Pantotheria, which do resemble the later mammals in many important respects. Passing over the taxonomic history of the group between 1824, when its first member (*Amphitherium*) was described, and 1871, one finds that even at the latter date the existence of the group as such was not recognized by Owen. In his classic memoir he grouped the pantotheres with such manifestly extraneous forms as *Microlestes* (*Thomasia*), *Spalacotherium*, and *Dromatherium*. At that time no adequate conception was possible of the truly vast gap between the Jurassic mammals and the Tertiary ones, whether measured in years or in evolutionary progress. It was possible for Owen to hope that bulky "ungulates and carnivores may still be found at Stonesfield or Durdlestone, or elsewhere."<sup>12</sup>

In 1880, Marsh named and defined the order Pantotheria, in the following words:

"With the exception of a very few aberrant forms the known Mesozoic mammals may be placed in a single order, which may appropriately be named Pantotheria. Some of the more important characters of the group would be as follows:

- (1) Cerebral hemispheres smooth.
- (2) Teeth exceeding or equaling the normal number, 44.
- (3) Premolars and molars imperfectly differentiated.
- (4) Canine teeth with bifid or grooved fangs.
- (5) Rami of lower jaw unankylosed at symphysis.

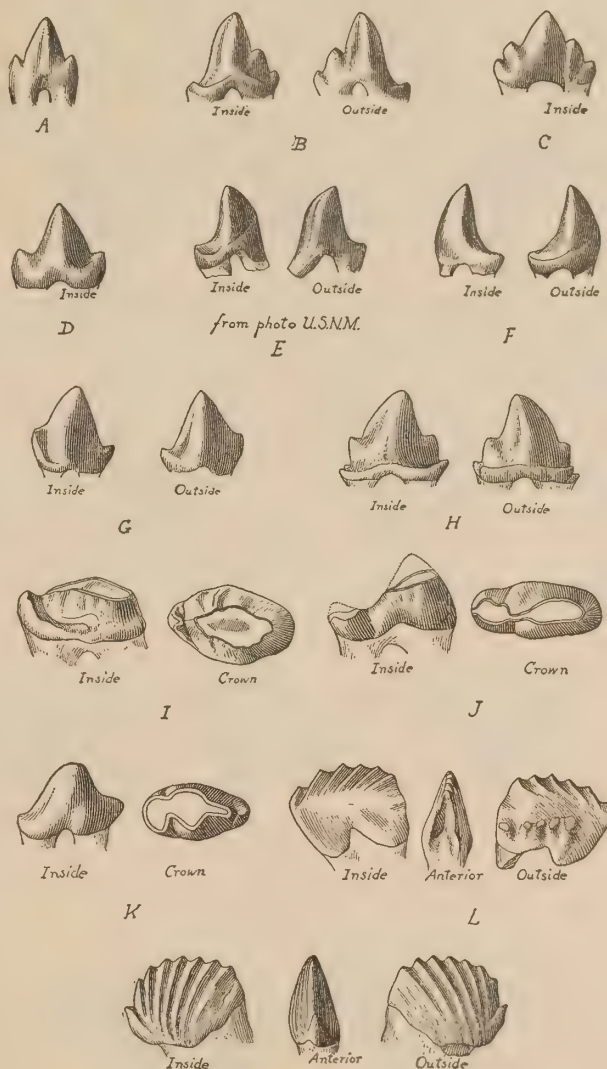


FIG. 20. Mesozoic mammals. Last lower premolars. A, *Amphilestes broderipii*. B, *Priacodon robustus*. C, *Amphidon superstes*. D, *Tinodon bellus*. E, *Paurodon valens*. F, *Laolestes eminens*. G, *Dryolestes priscus*. H, *Docodon victor*. I, Lance didelphodontine. J, Lance pediomyine. K, Lance insectivore. L, *Psalodon marshi*. M (bottom three drawings), *Meniscoëssus*. Not to scale.

<sup>12</sup> That is, elsewhere in the Jurassic. Stonesfield, Oxfordshire, is the locality of the middle Jurassic Stonesfield slate mammalian fauna, and the upper Jurassic mammalian fauna of the Purbeck beds comes from Durdlestone Bay in Dorsetshire.

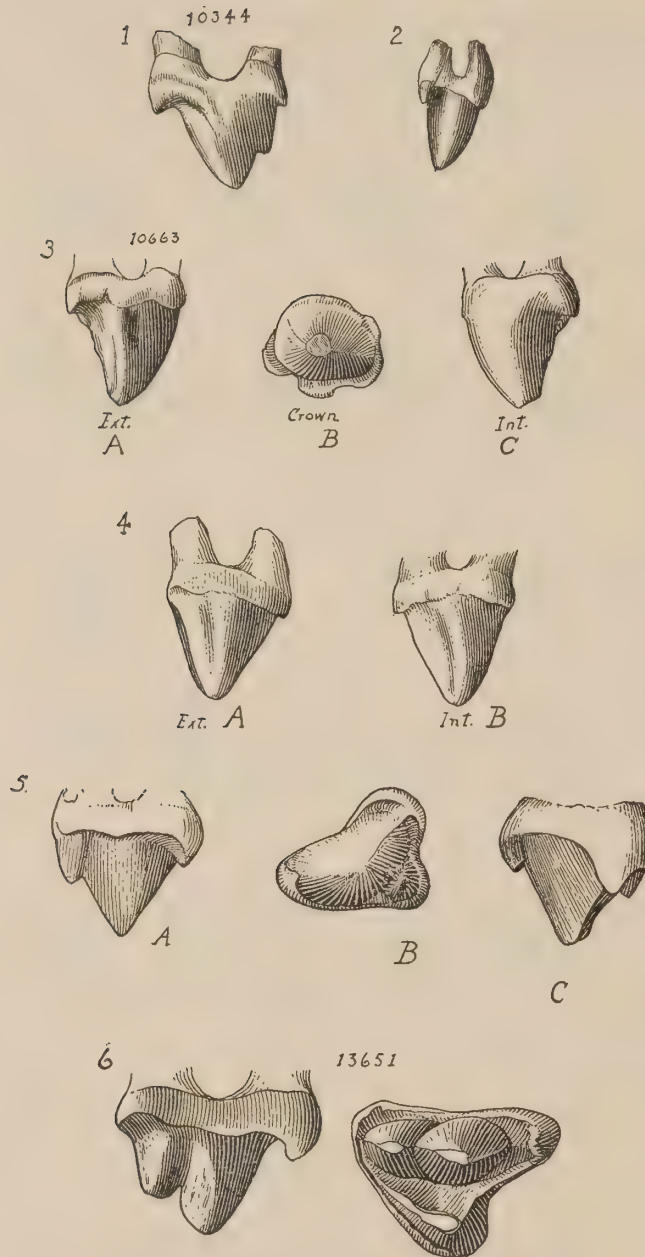


FIG. 21. Mesozoic mammals. Last upper premolars. 1, *Priacodon*. 2, *Peralestes*. 3, *Melanodon*. 4, *Herpetairus*. 5, *Docodon*. 6, *Gypsonictops*. Not to scale.

(6) Mylohyoid groove distinct on inside of lower jaws.

(7) Angle of lower jaw without distinct inflection.

(8) Condyle of lower jaw near or below horizon of teeth.

(9) Condyle vertical or round, not transverse.

The generalized members of this order were doubtless the forms from which the modern specialized Insectivores and Marsupials, at least, were derived."

As a matter of historical interest, not detracting from the importance of Marsh's recognition of the group for the first time, it may be noted that (1), while probably true, was not based on good evidence, that (2) and (4), as he later recognized, are open to exception, and that (3) and (8) are not strictly true.

As was noted in dealing with the Triconodonta, it is uncertain just how many Jurassic mammals were intended to be included in the Pantotheria. The natural inference from the arrangement of his paper of 1887 would be that he included all Jurassic mammals except the Allotheria. There can, however, be no doubt that the order was primarily based on the Dryolestidae. Although he specifically refers the Dromatheriidae to the Pantotheria, these, the triconodonts, and the symmetrodonts are excluded by his defini-

tion. In 1887 his views as to affinities were modified somewhat, as he then saw no marsupial characters in the order and considered it as possibly related to the Insectivora. Among forms now referred to the order, Marsh recognized the families Dryolestidae, "Diplocynodontidae," and Paurodontidae. In 1879 he had created a family Stylodon-



tidae, but he abandoned this in 1887, recognizing, as most subsequent writers have failed to do, that there is no difference between this supposed family and the Dryolestidae.

In his memoir (1888A) Osborn recognized five families: Amphitheriidae, Peralestidae, Kurtodontidae, Amblotheriidae, and Stylacodontidae. The first three were placed with the Triconodontidae in the Prodidelphia as marsupials and the last two in the Insectivora Primitiva as placentals. Later in the same year (1888B) he recognized the unity of the Jurassic mammals with tritubercular molars as opposed to those with triconodont molars and he abandoned the families Peralestidae and Kurtodontidae. In 1893 Osborn consistently grouped these mammals together, calling them trituberculates. In the same year the name Trituberculata Osborn, as a taxonomic term first appeared (Zittel 1893).

Despite some rearrangement of their contents, the orders Pantotheria Marsh and Trituberculata Osborn are synonymous. The question whether the prior term Pantotheria or the more widely adopted Trituberculata should be used for the group has been discussed in some detail elsewhere (Simpson 1928B, p. 108). It has been decided that the earlier name is not open to serious objection and is less misleading. The order is therefore called Pantotheria throughout the present work and its members pantotheres. "Trituberculate" is understood to be a term in dental morphology, applicable to members of various orders, and without taxonomic significance.

Four more classifications of the group may be given in brief *résumé*. That of Osborn in 1907 is as follows:

- Infraclass Placentalia
  - Order Pantotheria Marsh (Trituberculata Osborn)
    - Amphitheriidae
    - Amblotheriidae or Stylacodontidae
    - Paurodontidae
    - Diplocynodontidae

Gregory 1910:

- Subclass Theria
  - Infraclass Metatheria
    - ?Order Trituberculata (Pantotheria in part)
      - Amphitheriidae
      - Amblotheriidae (Stylacodontidae)
      - Paurodontidae
      - Dicrocynodontidae (Doubtfully placed here)

Gregory 1922:

- Order Trituberculata
  - Amphitheriidae
  - Stylodontidae
  - ?Diplocynodontidae

Schlosser in Zittel's *Grundzüge*, 1923 edition:

- Subclass Eplacentalia

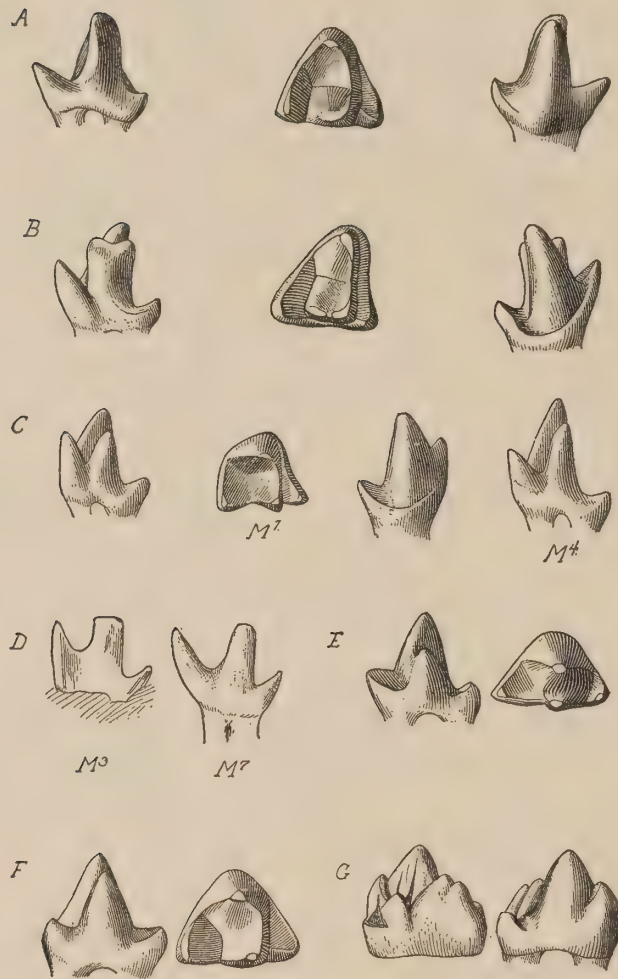


FIG. 22. Morrison pantotheres. Typical lower molars. A, *Dryolestes*, internal, crown, and external views. B, *Laolestes*, internal, crown, and external views. C, *Amblotherium*, internal, crown, and external views of  $M_1$ , and internal view of  $M_4$ . D, *Kepolestes*, internal views of  $M_3$  and  $M_7$ , without protoconid. E, *Archaeotrigon*, internal and crown views. F, *Tathiodon*, internal and crown views. G, *Docodon*, internal and external views. Not to scale.

## Order Marsupialia

## Suborder Polyprotodontia

6th Family: Pantotheriidae (Trituberculata, Pantotheria)<sup>13</sup>

Amphitheriinae

Amblotheriinae (Stylacodontidae)

Paurodontinae

Diplocynodontinae

The definitions and contents of the various families have been subject to much change, but since none of these recent classifications, or of others which might be quoted, was based on further original research it would serve no useful purpose to follow them in more detail here.

The molar structure of all of the genera of pantotheres is now clearly known. On this and on all the other available evidence is based the following outline classification:

## CLASS MAMMALIA Linnaeus 1758

## SUBCLASS THERIA Parker and Haswell

## ORDER PANTOTHERIA Marsh 1880

## Family Amphitheriidae Owen 1846

*Amphitherium* Blainville 1838

## Family Paurodontidae Marsh 1887

\**Paurodon* Marsh 1887*Peramus* Owen 1871\**Archaeotricon* Simpson 1927\**Tathiodon* Simpson 1927*Brancatherulum* Hennig 1927

## Family Dryolestidae Marsh 1879

\**Dryolestes* Marsh 1878\**Amblotherium* Owen 1871*Peraspalax* Owen 1871*Phascolestes* Owen 1871\**Laolestes* Simpson 1927\**Kepolestes* Simpson 1927

(Following genera based on upper jaws, possibly not all dryolestids):

*Kurtodon* Osborn 1887\**Herpetairus* Simpson 1927\**Melanodon* Simpson 1927\**Malthacolestes* Simpson 1927\**Euthlastus* Simpson 1927\**Miccylyotyrans* Simpson 1927\**Pelicopsis* Simpson 1927

<sup>13</sup> The whole group is inserted in the guise of a family (the name of which is invalid) between the Notoryctidae and Dasyuridae.



Family Docodontidae, new name.

\**Docodon* Marsh 1881

*Peraiocynodon* Simpson 1928

The genera marked \* occur in America, the others only in England, except *Bran-catherulum*, which is from East Africa.

## PAURODONTIDAE Marsh 1887

DEFINITION.—Cheek teeth  $P_4$   $M_4$  or less. Trigonid elongate, not compressed anteroposteriorly,  $me^d$  markedly lower than  $pr^d$ . Talonid not reduced, semicircular or triangular in plan, with one cusp, posterior or posterointernal in position. Lower molars supported by two large subequal roots. Lower jaw usually short and stout.

TYPE.—*Paurodon* Marsh.

DISTRIBUTION.—Purbeck beds, England. Morrison formation, Wyoming.

Founded for the single genus *Paurodon*, the validity of this family has been rather generally recognized. Gregory (1922), however, has provisionally united it with the Amphitheriidae, stating that its maintenance as distinct would depend on confirmation of Marsh's description of *Paurodon*. The present research has shown that Marsh was correct in all essentials and the family is therefore reinstated. The five genera placed here constitute a rather heterogeneous assemblage. *Archaeotrigon* is surely related to *Paurodon*. *Tathiodon* approaches the dryolestids in some respects, although the characteristic anteroposterior compression of the molars in the latter group is absent and the number of cheek teeth is markedly less. *Peramus* is widely distinct from the dryolestids, but is in many respects intermediate between the typical paurodontids and *Amphitherium*, so that its reference to the Amphitheriidae, where it has usually been placed hitherto, would be possible. *Bran-catherulum* is very poorly known, being based on a broken jaw without teeth, but it is probably closely allied to *Peramus*.

Aside from the aberrant Docodontidae, there are two families of pantotheres in the upper Jurassic: one, the Paurodontidae, with few molars, not compressed longitudinally, the other, the Dryolestidae, with many molars, compressed longitudinally. It might be supposed either that the dryolestid condition was primitive and the paurodontids have the molars secondarily elongated consonant with their reduction in numbers, or that the reverse is true, that the paurodontids are primitive and the dryolestids have the molars secondarily shortened consonant with their increase in numbers. The question is a theoretical one, not now possible of definitive solution, and somewhat outside the plan of the present memoir which is chiefly devoted to an exposition of what is positively known, but a few brief remarks on the subject are necessary, if only as a caution against unwarranted speculation. The probabilities at present seem strongly to favor the view that neither of these suppositions is true. It seems probable that the ancestral condition was one with many molars, not compressed longitudinally. From this type the paurodontids would seem to have been derived largely by reduction in

cheek tooth number, with retention or slight exaggeration of the elongate molars, and the dryolestids largely by anteroposterior compression of the molars with retention or slight exaggeration of the high cheek tooth number. A rather imperfect analogy is seen in the splitting of the Insectivora into the dilambdodont and zalambdodont groups. According to this view *Amphitherium* nearly represents the primitive conditions among Pantotheria. It is the earliest pantothere known and, as has been emphasized in the author's treatment of it (1928B), its characters are such that any other pantothere could be derived from it by changes which are of quite the same sort as have been demonstrated beyond doubt in other lines of mammals. In its high cheek tooth number it resembles the dryolestids, and in its relatively elongate molars it resembles the paurodontids, although without various minor specializations seen among the latter.

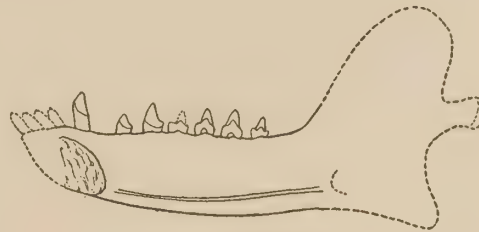
*Paurodon* Marsh 1887

1887. *Paurodon*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 342.

DEFINITION.—Dental formula  $I, C_1 P_2 M_4$ .  $Pa^d$  and talonid shelf-like, not forming true cusps,  $me^d$  very low. Talonid semi-circular in plan. With postcanine diastema, molars spaced. Horizontal ramus stout. Symphysis short. Coronoid arising some distance posterior to last molar.

TYPE.—*P. valens* Marsh.

DISTRIBUTION.—Morrison formation, Wyoming.



PAURODON

FIG. 23. *Paurodon*. Diagrammatic internal view of right lower jaw. Three times natural size.

*Paurodon valens* Marsh 1887

1887. *P. valens*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 342.

TYPE.—U.S.N.M. No. 2143. Left lower jaw with C,  $P_{1-2}$  and  $M_{1-4}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. First three molars each 1.2 mm. in length,  $M_4$  1.0 mm. in length.

DENTITION

The first tooth preserved is certainly a canine and not a premolar as suggested by Gregory (1922, p. 50). It is high, oval in section, with the tip excavated internally, and stands nearly erect, pointing but little forward. The root is also oval in section and is undivided. The longer axis of the section of the root is inclined outward anteriorly at about  $30^\circ$  to the long axis of the jaw.

Posterior to the canine is a diastema of about the same length, and then follow the six evenly spaced cheek teeth. The first of these has two roots, is laterally compressed, and has a posterior heel from which an internal cingulum runs forward and upward,

passing into the curved anterior cutting edge of the tooth. The main cusp is slightly recurved and there is no external cingulum. The crown is obviously that of a typical pantotherian premolar.  $P_2$  is closely similar, but somewhat larger.

$M_1$  resembles  $M_2$  save in being slightly longer and narrower, but it is somewhat worn and broken.  $M_2$  consists mainly of a single high external cusp with a convex posterior and external surface and a concave internal one, the two being separated by sharp anteromedian and posterointernal vertical angulations. The  $me^d$  is much smaller and lower than the main cusp and is internal and slightly posterior to the apex of the latter. Its separation from the base of the  $pr^d$  is imperfect and there is no trigonid basin. There is no true paraconid, its place being taken by a low shelf anterior to the  $me^d$ . The heel is little pronounced, sloping, not basined, with no true cusp.

$M_3$  is closely similar to the preceding tooth, but is a little higher, with slightly more pronounced cusps, the  $me^d$  directly internal to the  $pr^d$ .  $M_4$  is lower and less slender. The  $me^d$  is less marked and the  $pa^d$  and talonid are more nearly horizontal, but the latter is markedly smaller. All the premolars and molars have two subequal fangs, but on  $M_3$  the anterior root is a little the stouter.

The dental formula assigned to this specimen by Marsh, namely  $I, C_1 P_2 M_4$  is certainly correct. *Paurodon* has been cited as showing that the typical Tertiary dental formula was in existence as early as the Jurassic, but the grounds for this statement are difficult to see, as this formula is not that primitive for any later mammals. Neither  $P_3 M_4$  nor  $P_4 M_3$  is the correct formula for any known pantothere, although both occur among triconodonts.

#### MANDIBLE

The horizontal ramus is remarkably short and deep. The symphyseal surface is large, but shorter relatively than in the dryolestids, extending back to a point beneath  $P_1$ . The lower border of the ramus is slightly curved and is lowest beneath  $M_4$ . The internal groove is broad and shallow and converges slowly toward the lower border until it is beneath  $M_1$ , then runs parallel to the lower border to the symphysis. The external surface is evenly convex save where it is swollen above the root of the somewhat obliquely placed canine. There is one small mental foramen beneath the anterior root of  $P_1$ . A small part of the coronoid was shown by Marsh, but it is now missing. The anterior border of the coronoid arose some distance back of  $M_4$  at about  $45^\circ$  to the alveolar border. In this interspace there is room for another molar, but there is no trace of such a tooth although the individual appears to be adult or even old, and more than four molars do not occur in any close ally of *Paurodon*.

#### MEASUREMENTS

C	$P_1$	Lengths				$M_4$	Depth of ramus below $M_2$
		$P_2$	$M_1$	$M_2$	$M_3$		
1.0	0.8	1.2	1.2	1.2	1.2	1.0	3.7



*Archaeotrigon* Simpson 1927

1927. *Archaeotrigon*, Simpson, *Amer. Jour. Sci.* (5) XIII, 410.

DEFINITION.—Dental formula  $I_4 C_1 P_2 M_{3-4}$ . Paraconid low but distinct, talonid with low distinct cusp, metaconid intermediate in height. Talonid semicircular in plan. No postcanine diastema, molars not spaced. Horizontal ramus stout. Symphysis short. Coronoid arising immediately posterior to last molar.

TYPE.—*A. brevimaxillus* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

The paurodontids are, on the whole, the least satisfactorily known of the Morrison pantotheres. The specimens are so few in number and often so difficult of interpretation that a taxonomy built on them is purely provisional and subject to radical change if new and more complete material is discovered. *Archaeotrigon* is rather the best known of all. It is unquestionably close to *Paurodon*, yet it differs from the type (and only) specimen of the latter genus in characters which must be considered generic. At the same time, the possibility must be distinctly recognized that some of the differences between these two genera may be due to age differences or to faulty preservation. It is reasonably certain that the genera are distinct, but the distinctions may be either less or greater than here indicated. Two species are recognized.

*Archaeotrigon brevimaxillus* Simpson 1927

1927. *A. brevimaxillus*, Simpson, *Amer. Jour. Sci.* (5) XIII, 410.

TYPE.—U.S.N.M. No. 2793. Right lower jaw with C,  $P_{1-2}$ , and  $M_{1-2}$ .

REFERRED SPECIMEN.—Y.P.M. No. 13648. Left lower jaw in matrix, internal aspect, with  $P_{1-2}$ , and  $M_{2-3}$ , badly crushed.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Probably only three molars. Paraconid shelf narrow. Talonid relatively long.

## DENTITION

In the type specimen the dental formula is apparently  $I_4 C_1 P_2 M_3$ . The only question is whether another molar may not have appeared later in life. This seems rather improbable as the specimen seems fully adult and the base of the coronoid is immediately back of  $M_3$ , closer to this tooth than the coronoid is to  $M_4$  in *Paurodon*. In the related *A. distagmus*, however, there are apparently four molars, and the definitive number remains in doubt.

There are alveoli for four incisors, the first large and procumbent, the following ones progressively smaller and less procumbent. Unlike that of most pantotheres, the incisor series is not a straight anteroposterior line, but curves inward anteriorly.

The canine is much like that of *Paurodon*, so far as preserved, but the root has a shallow vertical median depression. The premolars also resemble those of *Paurodon*, although the internal cingulum, instead of passing into the anterior cutting edge

gently, meets the latter at an angle. The first two molars and alveoli for the third are preserved.  $M_2$  was the largest of the three. The molars differ sharply from *Paurodon* in the better development of the internal cusps. The  $pa^d$  is still small and low, but it is a well-defined cusp and not a mere sloping shelf. The  $me^d$  is larger and better defined than in *Paurodon*, and the heel is longer and bears a small but true cusp.

#### MANDIBLE

The horizontal ramus is smaller than that of *Paurodon* but of similar proportions. There are two mental foramina, low down on the mandible, one beneath the canine and one beneath  $P_1$ . The coronoid arises at about  $30^\circ$  immediately posterior to  $M_3$ . The internal groove is small and narrow.

#### MEASUREMENTS OF TYPE

C	Lengths:				Depth of ramus
	$P_1$	$P_2$	$M_1$	$M_2$	below $M_2$
1.0	0.9	1.2	1.2	1.6	3.4

#### *Archaeotricon distagmus*, new species

TYPE.—Y.P.M. No. 13641. Right lower jaw with  $M_{2-3}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Probably four molars. Paraconid shelf wider. Talonid shorter.

#### DENTITION

Imperfect as is the material on which the present species is based, it is of vital importance for the study of the paurodontids. Two molars are present and these are followed by alveoli for another, much smaller, molar. Two interpretations are possible, both accompanied by various difficulties. If the two molars are  $M_{1-2}$ , then  $M_1$  is larger than  $M_2$ , a unique character among pantotheres, and  $M_3$  is probably relatively more reduced than in *A. brevimaxillus*. If, as is more probable, these teeth are  $M_{2-3}$ , then there were four molars whereas it is probable that the genotype had only three. Provisionally adopting the latter alternative, the significance of the added molar is doubtful. It may (improbably) be due only to greater individual age, or to an individual anomaly, or to taxonomic distinction. Provisionally, it is considered as one of the characters distinguishing the species. Except for the fact that the paraconid shelf is wider, springing distinctly inward as well as forward, and that the heel is somewhat narrower, the molar structure is as in *A. brevimaxillus*.

#### MANDIBLE

The mandible is stouter than in the genotype and the internal groove is higher.

#### MEASUREMENTS

Length $M_2$	1.5 mm.
Length $M_3$	1.3 mm.
Depth of ramus below $M_2$	3.6 mm.

*Archaeotrigon* sp. indet.

MATERIAL.—Y.P.M. No. 13642. Lower jaw with last M.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

This specimen is of some interest in showing the last molar in *Archaeotrigon* and much of the posterior part of the mandible. The last molar is much like the preceding teeth in this genus, but smaller, being only 1.1 mm. in length and hence probably M<sub>4</sub>. The angular process is quite unlike that in the Dryolestidae and has much resemblance to *Peramus*. It is small, triangular, and projected downward and backward.

*Tathiodon* Simpson 1927

1927. *Tanaodon*, Simpson, *Amer. Jour. Sci.* (5) XIII, 410—non *Tanaodon* Kirk 1927.

1927. *Tathiodon*, Simpson, *Amer. Jour. Sci.* (5) XIV.

DEFINITION.—Cheek teeth six or seven. Paraconid distinct and stout, but not high. Talonid triangular in plan, with a posterointernal cusp. Metaconid higher, stouter, less sharply pointed than in *Archaeotrigon* or *Paurodon*. No postcanine diastema, molars not spaced. Horizontal ramus slender. Symphysis long.

TYPE.—*T. agilis* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

The name *Tanaodon*, originally applied to this genus, was given almost simultaneously but a little earlier to a Chinese Devonian mollusc. The mammal was therefore renamed *Tathiodon* two months after its original description. The molar type here displayed is more like that of the dryolestids than is that of any other paurodontid, but *Tathiodon* is at once distinguished from the Dryolestidae by the low number of cheek teeth and by the still relatively elongate molars, with roots unspecialized. A single species is known.

*Tathiodon agilis* (Simpson 1927)

1927. *Tanaodon agilis*, Simpson, *Amer. Jour. Sci.* (5) XIII, 410.

1927. *Tathiodon agilis*, Simpson, *Amer. Jour. Sci.* (5) XIV.

TYPE.—Y.P.M. No. 13649. Left lower jaw with two molars.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Lengths of two preserved molars, probably M<sub>2-3</sub>, 1.35 and 1.5 mm. respectively.

## DENTITION

The interpretation of alveoli is notoriously difficult, but an attempt is necessary in this case. At the anterior end of the jaw are three or four alveoli manifestly for incisors. Then follows an alveolus not larger than the following ones but not quite in line with them and pointing a little forward. This must have lodged the canine. Alveoli for two premolars follow, then there is a break from which the bone is missing, but since the



matrix impression of this part is known, there is little chance of error. The space is large enough to hold one tooth, whether premolar or molar. Next follow two well preserved molars. Posterior to these are alveoli for one more molar, then a space where the inner part of the jaw is broken revealing a cavity which may have lodged another, unerupted molar, although this is purely hypothetical. There were thus not less than six nor more than seven cheek teeth, of which probably two and certainly not over three were premolars. The formula may have agreed with that of *Paurodon* or of *Archaeotrigon distagnus*.

On the preserved molars, the paraconid points forward and upward and is as large as in *Dryolestes*. The metaconid is directly posterior to the  $pa^d$  and is only a little less high than the  $pr^d$ . The latter is sharply pointed but has a very broad base. The talonid is more of dryolestid than of paurodontid type, being low, with a distinct cusp directly posterior to the  $me^d$ . The trigonid, however, is longer than broad, the molars are supported by two equal roots, and the metaconid, while high for a paurodontid, would be low for a dryolestid.

#### MANDIBLE

The horizontal ramus is markedly more slender than in the two preceding genera and the symphysis is relatively longer. The internal groove is well marked and is parallel to the lower border where preserved.

#### MEASUREMENTS

Length $M_{2,3}$	1.35 mm.
Length $M_{3,3}$	1.5 mm.
Depth of ramus below $M_{3,3}$	2.5 mm.

### DRYOLESTIDAE Marsh 1879

DEFINITION.—Cheek teeth  $P_4$   $M_7$  or more. Lower molars with four cusps. Metaconid comparable to protoconid in height. Trigonid of middle molars shorter than broad, compressed anteroposteriorly. Talonid shorter than in *Amphitherium*, triangular in plan, with a single posterointernal cusp. Molars implanted by two very unequal roots, the larger external and anterointernal, the smaller posterointernal only. Lower jaw long and slender.

TYPE.—*Dryolestes* Marsh.

DISTRIBUTION.—Purbeck beds, England. Morrison formation, Wyoming and Colorado.

The various English and American genera referred to this family are very closely similar, in so far as they are based on lower jaws. Once the molar structure is completely known, indeed, the separation of the genera becomes much more difficult than was previously supposed and rests almost entirely on slight differences in the shapes, proportions, and placing of the cusps. With this strong resemblance before one, it is remarkable to find that they have almost never previously been placed in a single family. In 1879 Marsh proposed two families, the Dryolestidae and the Stylodontidae,

but in 1887 he united these under the former name, recognizing the unity of the group for the first and almost the only time. Osborn's first classification distributed the dryolestids in four families, *Peralestidae*, *Kurtodontidae*, *Amblotheriidae*, and *Stylacodontidae*, placed in two different orders and, indeed, subclasses. Later in the same year he suppressed the families *Peralestidae* and *Kurtodontidae* and recognized the fact that the dryolestids belonged in one order. In 1907 he finally united them in one family<sup>14</sup> but his definition still perpetuated the deeply rooted but erroneous idea that two quite different molar types are represented, one more normal, seen for example in *Amblotherium* itself, and one styloid, essentially with but one cusp and one root. The latest important classification, that of Gregory in 1922, unfortunately marked a step backward, for he referred some dryolestids to the *Amphitheriidae* and for others resurrected the name *Stylodontidae*. The latter family is doubly invalid, for it was founded in error, as Marsh quickly recognized, and was based on a preoccupied name.

This long persistence of what may now easily be shown to be a fundamental error is in no sense a reflection on the painstaking work on the group done by the authorities mentioned. It is rather a tribute to the unusual difficulty of the whole problem, to the absolute necessity of access to all the material and of removing concealing matrix when necessary, and to the need for the best optical aids. Previous to the splendid coöperation which now makes correction possible, no one worker had free disposal of the necessary materials and equipment. Marsh worked under the most advantageous conditions of the earlier students, and his final conception of the group was essentially correct.

The belief, then, has long been that certain genera of upper Jurassic pantotheres, the so-called *Stylodontidae* or *Stylacodontidae*, had much compressed, columnar molars with connate roots. In fact, the number and proportions of the cusps in these supposed genera are the same as in the typical dryolestids, the trigonid is, if anything, longer, the talonid is present and similar in character, and the two roots are developed in exactly the same way. Curiously enough, the typical genera of the two supposedly distinct groups, *Amblotherium* and *Stylodon*, are synonymous. Both were perforce examined with various cusps obscured by the matrix and *Amblotherium* was the internal, *Stylodon* the external, aspect of the same genus.

The discovery of this and of other similar errors

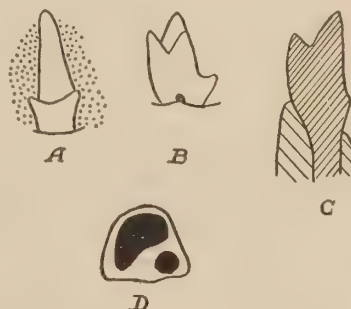


FIG. 24. Diagrams of dryolestid lower molar, essentially *Amblotherium*. A, external view, partly buried in matrix, so-called *Stylodon* or *Stylacodon*. B, internal view. C, transverse section, through protoconid. D, relation of roots (solid black) to crown (outline).

<sup>14</sup> Osborn, 1907, p. 23. He called the family "Amblotheriidae Osborn or Stylacodontidae Marsh." Marsh did not propose a family Stylacodontidae, however, and Amblotheriidae Osborn is identical with the earlier Dryolestidae Marsh. Osborn apparently abandoned the latter name because of his belief in the probable synonymy of *Dryolestes* and *Phascolestes*. Direct comparison shows these genera to be distinct, and there is no reason why the first name applied to the family, Dryolestidae, should not be retained.



has naturally resulted in a considerable decrease in the number of genera. Among the genera earlier based on lower jaws, only *Dryolestes*, *Amblotherium*, *Peraspalax*, and *Phascolestes* seem to be valid. Two genera have been added by the author. One, *Laolestes*, was previously included under *Dryolestes* which it closely resembles, and the other, *Kepolestes*, comes from a hitherto unmentioned locality for Jurassic mammals.

Perhaps the most gratifying result of the reëxamination of the magnificent Marsh Collection, however, has been the discovery of numerous pantothere upper jaws. A few fragments were known from the Purbeck beds, the best described in detail by Osborn under the name of *Kurtodon*. Marsh had named two upper jaws from the Morrison as species of *Dryolestes*, and Osborn (1904) had given accurate figures of two upper jaws, including one of Marsh's types, but unfortunately this material was, from a morphological point of view, the worst in the whole collection, with the molars badly worn and much broken. The only figure or detailed description of an adequately preserved Morrison pantothere upper molar was that of Gidley (1906, Pl. V, figs. 2-3). The apparent absence of such material was justly lamented, but when the Marsh Collection was overhauled, it was found that a large number of upper jaws, many still concealed in the matrix, had been set aside by Professor Marsh for future study. As will appear below, not only was the number of specimens surprisingly large, but they exhibited a most unexpected and welcome morphological variety.

The cataloguing and description of this material has involved a nomenclatural difficulty. In no case is there any association between these extremely important upper jaws and the lower jaws on which the whole nomenclature of the group has hitherto been primarily based. In the case of the triconodonts and docodontids, for instance, this lack of association is not serious, for here a study of occlusal relationships permits reasonably certain inference as to the taxonomic position of the upper jaws, but in dealing with the dryolestids this method also is unavailable. In no case are the proportions, dimensions, and occlusal relationships such that a definite type of upper molars could be referred with high probability to one genus of lower jaws and only one. Arbitrary reference to established genera would imply knowledge where none exists and, even if correct in some cases, would certainly be erroneous in others and would lead to almost ineradicable errors. Description of this fundamentally important material,—material which must inevitably gain an important place in many discussions involving the fundamental characters and early history of the Class Mammalia,—without applying names to it seems highly undesirable, if only from the point of view of convenience, which is, after all, the primary reason for the use of names. The question seemed of such importance that the advice of several eminent students of fossil mammals was sought and freely given. All agreed that the science would be best served by comparing the upper jaws carefully, dividing them into what appear to be natural genera, and applying new names to these genera regardless of the fact that some of these new names may, if associated specimens are found, be found to be synonymous with older names already applied to lower jaws only. There are excellent precedents for this course and it has proven to be entirely justified in the past by its usefulness,



even if only temporary. On the other hand, it was agreed that names of more than generic rank should not be based on unassociated upper jaws. This, also, has been done in the past but has proven often to have very unfortunate results.

In accordance with this decision six genera have been established on upper jaws: *Herpetairus*, *Melanodon*, *Malthacolestes*, *Euthlastus*, *Miccylo tyrans*, and *Pelicoptis*. These are all provisionally referred to the Dryolestidae. In the cases of *Herpetairus*, *Melanodon*, *Euthlastus*, and *Miccylo tyrans*, this reference is supported by much direct and indirect evidence and is probably correct. *Malthacolestes* and *Pelicoptis*, on the other hand, very possibly are not dryolestids. They may be paurodontids, or their rare remains may possibly represent genera or other groups otherwise unknown. In view of this doubt it seems best to associate them with the other upper jaws, with this word of caution. None of them are docodontids; the peculiar upper teeth of this family are well known and are referable to the genus *Docodon* with little possibility of error.

As here classified, the generic divisions within the family Dryolestidae are based primarily on molar structure. They are so drawn that a single unbroken and little worn molar may be referred to its correct genus in any given instance. Bearing in mind the fact that it is often impossible to distinguish between closely related Tertiary and recent genera from single teeth, this procedure has possibly resulted in drawing generic lines rather more broadly than is often done, but such a result requires no apology. It is more useful, at least in the present case, and does not greatly modify the modern concept of a genus.

### *Dryolestes* Marsh 1878

1878. *Dryolestes*, Marsh, *Amer. Jour. Sci.* (3) XV, 459.

1887. *Asthenodon*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 336.

DEFINITION.—Dental formula  $I_4 C_1 P_4 M_8$ . Premolars with discontinuous internal cingulum, with distinct anterior accessory cusp. Metaconid of molars columnar, not bifid; paraconid slightly procumbent, lower than  $me^d$ ;  $pa^d$ ,  $me^d$ , and talonid cusp in a straight longitudinal line. No external cingulum.

TYPE.—*Dryolestes priscus* Marsh.

TYPE OF *ASTHENODON*.—*Asthenodon segnis* Marsh = *Dryolestes priscus* Marsh.

DISTRIBUTION.—Morrison formation, Wyoming.

As mentioned again below, Marsh's figure of "*Dryolestes priscus*" (1887, Pl. IX, fig. 2) was not, as has since been supposed, of the genoholotype but of a referred specimen which proves on further study to belong to a distinct genus. Even more curious and unfortunate is the history of the supposed genus "*Asthenodon*." *Asthenodon* was differentiated from *Dryolestes* by Marsh on the more uniform size of the tooth series and the presence of three, rather than four, premolars. Careful measurement, after more complete preparation, shows that the teeth do not differ from *Dryolestes* in size. The supposed presence of but three premolars was also a very natural error. In the type of *Asthenodon segnis*, the first tooth is not a canine, as first stated, but a premolar which had become loose and was unnaturally far out of the alveolus when buried.

Except for this abnormal, post-mortem extrusion, it agrees in every detail with  $P_1$  of *Dryolestes*. Marsh's referred specimen (1887, Pl. IX, fig. 6) shows the true canine, but is broken off just back of  $P_2$  and hence did not draw his attention to his error. Marsh explicitly pointed out that the "molars agree in general form with those of *Dryolestes*." His figure was drawn from the specimen as it lay half buried in matrix, with the cusps partly hidden, and hence might be imagined to contradict his correct interpretation of the molars in his text. Following the figure rather than the text, Osborn stated (1888A, p. 238) that "The molars resemble those of *Dryolestes*, but lack the third postero-internal cusp." This has ever since been accepted as true and has been supposed by Osborn, Winge, Gregory, and others to show that *Asthenodon* forms a link between the heelless symmetrodonts and the typical dryolestids. Cleared of the matrix, the molars substantiate Marsh's view that they were of dryolestid type, and *Dryolestes* and *Asthenodon* prove to be synonymous.

Only one species of *Dryolestes* can now be recognized. In 1879 (p. 215) Marsh named a supposed second species *Dryolestes vorax*, distinguished as being smaller, with the horizontal ramus more slender, less curved, and less compressed. The holotype. Y.P.M. No. 11818, has but one tooth which proves on restudy to be a first molar of docodont type (the docodontids had not then been discovered save for this imperfect example). *Dryolestes vorax* is a *nomen nudum*, the type not being specifically identifiable. In 1887 (Pl. IX, fig. 3) Marsh figured a good lower jaw as *Dryolestes vorax*, but this specimen is not conspecific, or even congeneric, with the holotype. It is probably referable to *Laolestes eminens*—the teeth are strongly worn and slight differences from the type of the latter species are probably due entirely to this cause.<sup>15</sup>

Marsh also created a species *Dryolestes gracilis*. The species is valid, but must be referred to *Amblotherium*. In the latter genus it becomes a homonym. It is treated below under the name *Amblotherium debilis*.

### *Dryolestes priscus* Marsh 1878

1878. *Dryolestes priscus*, Marsh, *Amer. Jour. Sci.* (3) XV, 459.

1880. *Stylacodon validus*, Marsh, *Amer. Jour. Sci.* (3) XX, 236.

1887. *Asthenodon segnis*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 336.

TYPE.—Y.P.M. No. 11820. Fragment of right lower jaw with one molar.

<sup>15</sup> It has been generally assumed that the specimens figured in Marsh 1887 as representative of the various species are the types of those species. In some instances this is incorrect, as reference to the original descriptions would have indicated. It has been possible to identify the type specimens of the various species beyond any question, the original descriptions, Marsh's notations with the specimens, and a manuscript list of types in his hand furnishing a triple check. Merrill's *Catalogue of Types . . . in the Department of Geology, United States National Museum* lists as types (i.e., holotypes) several Mesozoic mammal figured specimens which are referred, not original types. Pt. II, p. 21, No. 2138 is not the type of *Allacodon pumilus*. P. 24, No. 2862, paratype, or referred specimen, not cotype of *Asthenodon segnis* (Marsh designated a type and specifically said that this specimen was referred). P. 35, No. 2727, not type of *Dryolestes vorax*, as just pointed out above. P. 61, No. 2693, not type of *Stylacodon gracilis* but a later specimen, treated by Marsh in the same way as No. 2727.



NEOTYPE.—U.S.N.M. No. 2722. Right lower jaw with  $P_{2-4}$  and  $M_{1-7}$ .<sup>16</sup>

TYPES OF SYNONYMS.—*Stylacodon validus*: Y.P.M. No. 11884. Right lower jaw with  $P_{3-4}$  and  $M_{1-4}$ . *Asthenodon segnis*: Y.P.M. No. 10646. Right lower jaw in matrix, crushed, external aspect, with  $P_{1-4}$  and  $M_{1-7}$ . Fig'd Marsh 1887, Pl. IX, fig. 7.

HORIZON AND LOCALITY.—Morrison formation, Como Bluff, Wyoming. The type was found at the north end of the bluff, just under the sandstone capping, hence at a higher level than any other mammals from this locality. The other specimens are from Quarry 9, with a single exception.

DIAGNOSIS.—Sole species of the genus. Dimensions as below.

This was the first Mesozoic mammal found. Like most harbingers of new fields, the type is very imperfect. The single tooth preserved is badly worn and lacks the main cusp. After prolonged study and careful comparison, it has seemed possible to designate a proper neotype with sufficient probability, thus saving this historic and widely used name. Marsh's figured specimen (1887, Pl. IX, fig. 2), Y.P.M. No. 13719, cannot be accepted as the neotype. It was not so designated by Marsh, and it seems improbable that it is congeneric with the type. Certainly it is not congeneric with the specimen here made neotype.

*Stylacodon validus* was described when neither *Stylacodon* nor *Dryolestes* were well known. It would have been withdrawn from the former genus had Marsh ever revised the group, for it shows none of the characters given by him as characteristic of *Stylacodon*, while, as he said, the molars agree with those of *Dryolestes*. It shows no specific differences from the neotype.

When the supposed generic characters of *Asthenodon* are recognized as erroneous, there remain no specific distinctions between *Asthenodon segnis* and the neotype of *Dryolestes priscus*.

#### DENTITION

The crowns of the incisors and canine are not known in this genus, but they were probably much like those of the related *Laolestes*. The premolars, four in number, are of identical pattern, but differ in size and proportions.  $P_1$  and  $P_2$  are of about the same size.  $P_3$  is somewhat larger and higher, about equaling  $M_1$  in height, while  $P_4$  is notably the largest tooth of the premolar series, overtopping the first molar. The external surface of each tooth is convex. There is a small anterior accessory cusp near the tip of the high somewhat recurved main cusp. From this accessory cusp there runs down on the internal surface a sharp vertical crest separated from the base of the main cusp by a short vertical valley. The crest curves somewhat posteriorly at its lower end but disappears without crossing the base of the main cusp. Back of the main cusp at a low level is a small posterior cusp or heel. Its inner surface is also sharply separated from that of the main cusp and the internal ridge running downward from it curves forward and becomes horizontal inferiorly before disappearing.

<sup>16</sup> Through inadvertence, Y.P.M. No. 10646 (type of *Asthenodon segnis*) was given as the neotype in *Amer. Jour. Sci.* (5) XIII, 411.



M<sub>4</sub> and M<sub>5</sub> are the largest and highest of the molars, the series decreasing gradually both ways from these. All of the molars are closely similar in structure, and are of very primitive tuberculosectorial type, with distinct trigonid and talonid. The trigonid consists of the three primitive cusps only. The pr<sup>d</sup> is high, simple, and vertical, approximately conical but sending toward the pa<sup>d</sup> and toward the me<sup>d</sup> distinct shearing crests which begin at its apex as angulations in the otherwise circular horizontal section. The me<sup>d</sup> is directly internal to the pr<sup>d</sup>, apparently a trivial feature but probably one of much functional and evolutionary significance. The me<sup>d</sup> is simple, columnar, bluntly pointed, and is connected with the pr<sup>d</sup> by a shearing transverse crest as already noted. This crest bears a deep V-shaped notch between the pr<sup>d</sup> and me<sup>d</sup>. The pa<sup>d</sup> springs forward and upward at an angle of about 45°. It is united to the pr<sup>d</sup> by an oblique, notched, transverse crest, and its base reaches that of the me<sup>d</sup> so that the trigonid is basined. The pa<sup>d</sup> is much lower than either of the other cusps. On M<sub>1</sub> the trigonid is about as long as broad, but on the succeeding molars it becomes progressively more compressed anteroposteriorly, reaching a maximum on M<sub>6</sub>. Wear on the trigonid is of two types: The oblique anterior border of the tooth, involving the pa<sup>d</sup>, pr<sup>d</sup>, and the crest between them is worn by shear, developing a facet at an angle of about 75° to the horizontal, and a second facet of wear at about the same angle, but dipping posteriorly, involves the posterior side of the pr<sup>d</sup>, the me<sup>d</sup>, and the crest between them. With more advanced wear these two surfaces become confluent and more horizontal, truncating the whole trigonid.

The talonid is narrow, but is present on all molars. First appearing very low on the crown beneath the pr<sup>d</sup>-me<sup>d</sup> notch, it runs inward and upward, widening as it goes, and culminates in a low cusp directly posterior to the me<sup>d</sup>. It is not basined.

Each molar has two roots. One is very small and is confined to the posterointernal part of the tooth, below the talonid cusp. The other is large and supports the antero-internal and whole external part of the tooth. In internal view two apparently equal roots are thus seen, while in external view but one appears.

#### MANDIBLE

The horizontal ramus is long and slender, the alveolar border nearly straight in the molar region, the lower border gently convex. The symphyseal surface, where union was ligamentous or cartilaginous only, is long, ending posteriorly beneath P<sub>3</sub>. The internal groove is well marked. It begins just anterior to the dental foramen and runs forward to the symphysis, gradually converging toward but not reaching the lower border. The coronoid process is incompletely known, but was apparently long and high. The masseteric fossa is broad and shallow and not sharply delimited. The dental foramen is at the extreme anterior end of the equally shallow pterygoid fossa. The angle is sharply differentiated, but is small, styloid, and projects straight backward, continuing the curve of the lower border. There is apparently but one mental foramen, beneath the posterior root of P<sub>2</sub> and anterior root of P<sub>3</sub>.

## MEASUREMENTS OF NEOTYPE

Lengths:

P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>	M <sub>5</sub>	M <sub>6</sub>	M <sub>7</sub>	M <sub>8</sub>
..	..	1.0	1.3	1.3	1.4	1.5	1.6	1.6	1.4	1.3	..

Depth of ramus below M<sub>4</sub>, inside 4.2

The molar series is crowded, each pa<sup>d</sup> somewhat overlapping the preceding talonid, so that the total measurement is less than the sum of the individual teeth and is usually much modified by slight crushing.

*Laolestes* Simpson 1927

1927. *Laolestes*, Simpson, *Amer. Jour. Sci.* (5) XIII, 411.

DEFINITION.—Dental formula I<sub>4</sub> C<sub>1</sub> P<sub>4</sub> M<sub>8</sub>. Premolars with continuous internal cingulum, without anterior accessory cusp. Metaconid of molars columnar, bifid at apex; paraconid slightly procumbent, lower than me<sup>d</sup>; pa<sup>d</sup> and talonid cusp distinctly internal relative to me<sup>d</sup>. External cingula on molars.

TYPE.—*Laolestes eminens* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

This is the most common single form in the Morrison mammalian fauna. Although clearly quite distinct, it is close to *Dryolestes* in size and in general character. The relatively few specimens which are really attributable to *Dryolestes* were not closely studied or entirely cleaned by Marsh, as the better jaws of the present genus seemed to be more satisfactory, and consequently most of our supposed knowledge of *Dryolestes* was formerly based on *Laolestes*. Besides the more common form, the genotype *L. eminens*, which varies somewhat, there is a clearly distinct second species, here described as new.

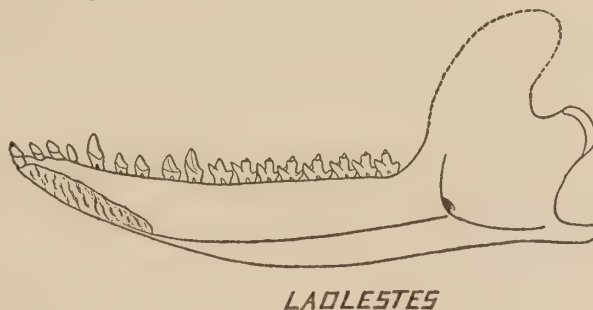


FIG. 25. *Laolestes*. Diagrammatic internal view of right lower jaw. Three times natural size.

*Laolestes eminens* Simpson 1927

1927. *L. eminens*, Simpson, *Amer. Jour. Sci.* (5) XIII, 411.

TYPE.—Y.P.M. No. 13719. Left lower jaw in matrix, inner aspect, with I<sub>3-4</sub>, C, P<sub>1-3</sub>, and M<sub>1-8</sub>—one of the finest known mammal jaws from the Mesozoic. Fig'd (as *Dryolestes priscus*), Marsh 1887, Pl. IX, fig. 2.

PRINCIPAL REFERRED SPECIMENS.—Y.P.M. No. 10662. Left lower jaw with P<sub>4</sub> and M<sub>1-4</sub>.

U.S.N.M. No. 2727. Left lower jaw with C, P<sub>2-4</sub> and M<sub>1-7</sub>, much worn. Fig'd (as *Dryolestes vorax*), Marsh 1887, Pl. IX, figs. 3-4.

The following less important specimens have also been studied and referred to this species and may be listed for the convenience of possible future workers:

Y.P.M. Nos. 10658, 10660, 10661, 13720, 13721, 13723, 13724, 13725, 13726.

U.S.N.M. Nos. 2729, 2731, 2732.

A.M.N.H. No. 3001. Fig'd (as *Phascolestes vorax*), Osborn 1907, fig. 31.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Length M<sub>4</sub>, 1.2-1.4 mm. Inner surface of paraconid smooth. Trigonid strongly basined.

This abundant species shows considerable variation, and it may be possible to subdivide it at some later date. The molar size may vary as much as 15 per cent, the length of the trigonid and bulk of the metaconid vary slightly, and the size of the premolars relative to the molars also varies. These and a few other slight differences could easily be due to wear, to crushing, or to individual or sexual differences.

#### DENTITION

The anterior incisor is large and procumbent, the following progressively smaller and less procumbent, and they form an almost straight anteroposterior series. Each has a single stout cylindrical root. The tip of each is spatulate, rounded, convex externally and excavated internally above the basal swelling.

The canine is a moderately stout, somewhat procumbent tooth implanted by two quite distinct roots, the posterior a little more oblique and larger. The anterior profile of the crown is strongly convex, the posterior somewhat concave. The external face is convex, the internal excavated above the slight cingulum, which runs forward from the small heel and merges with the anterior border.

The premolars resemble the canine rather closely in morphology and are also like those of *Dryolestes* save that there is no anterior accessory cusp and the cingulum is continuous, running forward internally from the small heel to curve into the anterior border. P<sub>1</sub> is small, the following premolars progressively larger until P<sub>4</sub> is of about the same size as the canine. As in all dryolestids the change from the tall trenchant P<sub>4</sub> to the lower tuberculosectorial M<sub>1</sub> is very abrupt. There is no trace of the supposedly gradual transition which these mammals have been supposed to show. They are farther from a homodont condition than most later mammals.

The eight molars are of nearly equal size, although they decrease slightly both ways from M<sub>6</sub>. Each has the same elements in nearly the same relationships as in *Dryolestes*. The metaconid is remarkable. It does not rise to a bluntly pointed apex, as in *Dryolestes*, but is columnar, usually somewhat expanded at the tip, and the apex, when unworn, is bifid, divided into distinct anterior and posterior points. These are separated by a small vertical furrow which runs from the apex down toward the trigonid basin. This character is least marked on M<sub>1</sub> and M<sub>8</sub> but may be seen on all when unworn. The talonid is of the same general character as in *Dryolestes*, but instead of



becoming obsolete beneath the  $pr^d$ - $me^d$  notch in passing externally, it continues, becoming narrower and lower on the crown, and passes into a low and rounded horizontal external cingulum on the base of the  $pr^d$ . On the middle cheek teeth the  $pa^d$  and talonid cusp are not in line with the  $me^d$ , as in *Dryolestes*, but are somewhat internal to it and are connected across its base by a nearly horizontal swelling. This character is first definitely indicated on  $M_8$ , reaches a maximum on  $M_6$  or  $M_7$ , and is slightly less again on  $M_8$ . On all the molars, except as modified by wear, the  $me^d$  is very slightly lower than the  $pr^d$ .

#### MANDIBLE

The mandible is very like that of *Dryolestes*, and its general characters vary but little within the family. In dealing with dryolestid lower jaws the marked differences between the internal and external aspects have often proven to be a stumbling block. These differences are very clearly brought out in the present material. The internal surface is flattened and the mouths of the alveoli are here higher than externally. The external aspect is rounded, with the mouths of the alveoli lower. Thus when only the inner side is visible one apparently has a very stout jaw with low molars implanted by two roots, while in external aspect there is apparently a slender jaw with high molars implanted by only one root.

The coronoid is somewhat confusing in the published figures of the type jaw (e.g., Marsh 1887, Pl. IX, fig. 2) as it is here much broken. Actually it arose immediately back of  $M_8$ , was high, broad, and somewhat recurved. The condyle is somewhat above the alveolar level, as in all pantotheres, and has an articular surface of irregular oval shape.

The angle is of dryolestid type, small, styliform, not at all compressed transversely, separated from the condyle by a large semicircular notch. The pterygoid fossa is bounded below by a low sharp pterygoid crest, and has the dental foramen at its anterior end, but little posterior to the last molar. On Y.P.M. No. 10662 there is a mental foramen beneath the posterior root of  $P_1$ . This specimen also has the internal groove discontinuous, interrupted beneath  $M_4$ —an individual variation.

#### MEASUREMENTS

Lengths:

	$P_1$	$P_2$	$P_3$	$P_4$	$M_1$	$M_2$	$M_3$	$M_4$	$M_5$	$M_6$	$M_7$	$M_8$
Y.P.M. 13719	0.7	0.8	0.8	..	1.1	1.1	1.2	1.2	1.3	1.3	1.2	1.2
Y.P.M. 10662	..	..	..	1.4	1.1	1.2	1.3	1.3	..	..	..	..
U.S.N.M. 2727	..	1.0	1.1	1.1	1.1	..	..	..	..	1.4	..	..
Y.P.M. 13720	..	..	..	..	..	..	1.2	1.4	1.4	1.4	1.3	..

Y.P.M. 13719: Depth of ramus below  $M_8$ , inside 4.0

Length  $P_1$ - $M_4$  13.3

Anterior end to tip of angle *ca.* 28.0

Y.P.M. 10662: Depth of ramus below  $M_4$   $\left\{ \begin{array}{l} \text{inside} \\ \text{outside} \end{array} \right.$   $\left. \begin{array}{l} 3.8 \\ 3.0 \end{array} \right.$

*Laolestes grandis*, new species

TYPE.—Y.P.M. No. 13727. Part of right lower jaw with  $M_{1-4}$ , broken.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Molars about 35 per cent larger than in *L. eminens*. Paraconid shelf less distinctly basined. Sharp, somewhat nodulated crest running down posterointernal slope of  $pa^d$  and nearly meeting a similar crest running forward from talonid cusp.

## DENTITION

This species rests on a single specimen of very indifferent preservation, but it is so clearly distinct from *L. eminens* that its description is obligatory. It is not certain that the metaconid tip was bifid, but as the other characters of the species are such as to accentuate the difference from *Dryolestes* it is reasonable to assume that this distinctive character of *Laolestes* was also present. On  $M_4$  the  $pa^d$  and talonid cusp are quite as internal as in the corresponding tooth of *L. eminens*. The  $pa^d$  is more sharply pointed and the paraconid shelf, or trigonid basin, is less distinctly basined than in *L. eminens*. Down the posterointernal face of the  $pa^d$  runs a small sharp crest, somewhat discontinuous or nodulated, which passes onto the internal face of the base of the  $me^d$  where it nearly but not quite reaches a similar crest running forward from the talonid. A similar ridge may be seen on the talonid of *L. eminens*, although not distinct so far forward as  $M_4$ , but such a character has not been observed on the  $pa^d$  of that species.

## MEASUREMENTS

Length $M_1$	ca. 1.6
Length $M_3$	ca. 1.7
Length $M_4$	1.7
Depth of ramus below $M_4$ inside	4.4

? *Laolestes* sp. indet.

MATERIAL.—U.S.N.M. No. 2862. Anterior portion of left lower jaw, with  $I_{1-4}$ , C, and  $P_2$ . Fig'd (as *Asthenodon segnis*), Marsh 1887, Pl. IX, fig. 6.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

This interesting fragment was referred by Marsh to his *Asthenodon segnis*,<sup>17</sup> but the apparent basis of the reference, supposed resemblance of the canine, was inadequate, as the canine is not present in the type of this synonym of *Dryolestes priscus*. It is uncertain whether it should be referred to *Dryolestes* or to *Laolestes*, more probably to the latter. The two genera were apparently closely similar in this region.

The incisors and canine are beautifully displayed in external view and are as in *Laolestes eminens*. There are two mental foramina, one beneath  $I_4$  and C, the other beneath  $P_2$ .

<sup>17</sup> It has been erroneously supposed to be a cotype. Marsh (1887, p. 336) specifically states that his Pl. IX, fig. 7 is the type and that this is referred.

*Amblotherium* Owen 1871

1866. *Stylodon*, Owen, *Geol. Mag.*, III, 199. Non *Stylodon* Beck 1837.  
 1871. *Amblotherium*, Owen, *Mem. Mes. Mam.*, 29.  
 1871. *Achyrodon*, Owen, *Mem. Mam. Mes.*, 37.  
 1879. *Stylacodon*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 60.  
 1887. *Laodon*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 337.  
 1898. *Odontostylus*, Trouessart, *Cat. Mam.*, 1247. Non *Odontostylus*, Gray 1840.  
 1899. *Trouessartia*, Cossman, *Rev. Crit. Pal.*, May 1899, 30. Non *Trouessartia*, Canestrini & Kramer, Jan. 1899.  
 1899. *Trouessartella*, Cossman, in Trouessart, *Cat. Mam.*, 1433.

DEFINITION.—Dental formula  $I_4 C_1 P_4 M_{7-9}$ . Premolars similar to those of *Laolestes*, slender, recurved, with no anterior accessory cusp. Metaconid of molars simple, pointed; paraconid erect, nearly or quite as high as  $me^d$  on posterior molars, separated from  $me^d$  by a deep V-shaped notch;  $pa^d$ ,  $me^d$  and talonid cusp in a straight antero-posterior line. External cingulum on molars (faint in one English species). Small forms with very slender jaws with pointed, recurved, hook-like coronoid processes.

TYPE.—*Amblotherium soricinum* Owen.

DISTRIBUTION.—Purbeck beds, England. Morrison formation, Wyoming.

Owen's three genera *Stylodon*, *Amblotherium*, and *Achyrodon* have elsewhere been shown to be synonymous (Simpson 1928B, p. 129). *Stylodon* was proposed first, but it was preoccupied. It was based on the external view of the lower jaw, *Amblotherium* on the internal view with the protoconid revealed but the metaconid broken, *Achyrodon* on the internal view with the protoconid hidden and the metaconid complete. Eight years after

Owen's memoir, in which he still recognized all three genera, Marsh discovered an American ally which he named *Stylacodon*, and when another eight years had passed, in his final summing up of 1887, he named another genus, *Laodon*. In his great memoir, Osborn considered *Stylodon* and *Stylacodon* as synonymous.<sup>18</sup> Not recognizing this synonymy, which was quite correct, Trouessart in 1898 proposed to replace *Stylodon* by *Odontostylus*. The latter name was also preoccupied, and Cossman in 1899 proposed replacing it by *Trouessartia*, but this in turn proved to be preoccupied, and was finally replaced by *Trouessartella*. Three additional names were thus applied to a genus which had already been given five separate names, one preoccupied and four unpreoccupied but synonymous.

*Laodon* was characterized by Marsh as follows:

1. Metaconid greatly reduced in size.

<sup>18</sup> He follows the procedure, not sanctioned by later usage, of using Marsh's name for the genus but ascribing it to Owen, who first described the same form but under a preoccupied name. He calls it "*Stylacodon*, Owen, 1866" but draws attention to its correct taxonomic history in a footnote.

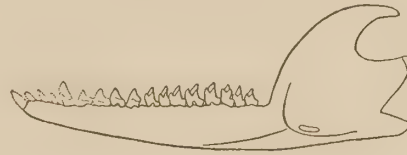


FIG. 26. *Amblotherium*. Diagrammatic internal view of right lower jaw. Three times natural size.



2. Five premolars.
3. Constriction behind molar teeth stronger than in *Stylacodon*.
4. Jaw deeper below molars.
5. Lower margin convex, as in *Dryolestes*.

None of these characters is valid. 1 is due to wear and to breakage. 2 was based on inadequate evidence and is surely erroneous. 3 must have been due to incomplete preparation, as there is now no postmolar constriction in either "*Stylacodon*" or "*Laodon*." 4 is due wholly to the fact that the inner rather than the outer aspect of the jaw is presented. As regards 5, it is true that the preservation of different parts, seen in different aspects, in the two cases gives a different appearance, but the superposition of accurate tracings from enlarged photographs shows that there is actually no significant difference in the form of the jaw, or in any other character. *Laodon* and *Stylacodon* are certainly synonymous. This American genus cannot now be distinguished from the English *Amblotherium-Achyrodon-Trouessartella* ("*Stylodon*") and for the present, at least, all must be referred to *Amblotherium*, the earliest valid name applied to the genus. This reduction of five generic names to synonymy has resulted also in a reduction of the number of species. Two species, *A. soricinum* and *A. nanum*, are recognizable in the English Purbeck beds and two, *A. gracilis* and *A. debilis*, in the American Morrison formation. *Stylacodon validus* Marsh, as already pointed out, is a synonym of *Dryolestes priscus*.

#### *Amblotherium gracilis* (Marsh 1879)

1879. *Stylacodon gracilis*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 60.

1887. *Laodon venustus*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 337.

1927. *Amblotherium gracilis*, Simpson, *Amer. Jour. Sci.* (5) XIII, 412.

TYPE.—Y.P.M. No. 11883. Left lower jaw, in matrix. Anterior fragment, toothless, inner aspect. Middle portion, matrix impression only. Posterior portion, outer aspect, with  $P_4$ ,  $M_{1-4}$ .  $P_3$  preserved separately.

TYPE OF *LAODON VENUSTUS*.—U.S.N.M. No. 2142. Left lower jaw in matrix, inner aspect, with  $P_{3-4}$  and  $M_{1-7}$ . Fig'd, Marsh 1887, Pl. IX, fig. 5.

PRINCIPAL REFERRED SPECIMENS.—U.S.N.M. No. 2693. Left lower jaw in matrix, outer aspect, with  $P_4$  and  $M_{1-8}$ . Fig'd (as *Stylacodon gracilis*), Marsh 1887, Pl. IX, fig. 1.

Y.P.M. No. 13732. Right lower jaw with  $M_{5-7}$ .

Y.P.M. Nos. 13731 and 13733 are also tentatively referred.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Length of molar series about 6.0 mm., molars 20-25 per cent larger than in *A. debilis*. External cingulum strong.  $Pa^d = me^d$  on  $M_{6-7}$ .  $M_7$  nearly as large as  $M_6$ .

#### DENTITION

The four premolars agree in most respects with those of *Laolestes*, save in their smaller size. Each has a single high somewhat recurved main cusp with a small pos-

terior heel. The external surface is convex, the internal one excavated above the cingulum, which runs forward from the small heel and curves into the anterior shearing edge without forming an anterior accessory cusp.

The molars, also, are of the now familiar dryolestid type, differing only in details from those of *Dryolestes* or *Laolestes*. The so-called "stylodont" molar type, high, slender, piercing, with confluent roots, so familiar in the literature, did not occur in nature. As in all dryolestids, the  $pr^d$  is high and sharply pointed. The  $me^d$  is slightly lower, erect, tapering to a fairly sharp point, unlike that of the two preceding genera when unworn. The  $pa^d$  differs most significantly from that of either *Dryolestes* or *Laolestes*, as it is not at all procumbent. Its anterior contour is vertical. On the anterior molars it is lower than the  $me^d$  in about the same proportion as the latter is lower than the  $pr^d$ , but on the largest and most characteristic molars,  $M_{6-7}$ , the paraconid is of about the same height as the metaconid.  $Pa^d$  and  $me^d$  are separated by a deep, narrow, V-shaped notch. The anteroposterior compression of the trigonid is progressive from  $M_1$  to  $M_6$  or  $M_7$  as in other dryolestids, but the trigonid basin is at least as long as in any other dryolestids, contrary to the usual statement. On  $M_3$  it is about as broad as long, posterior to this the breadth exceeds the length.

The talonid, again contrary to the usual statement for "*Stylacodon*," is always present and is at least as well developed as in *Dryolestes* or *Laolestes*. As in those genera, it is triangular in plan, bearing a single cusp which is here directly posterior to the  $me^d$ , and narrowing as it passes outward and downward on the crown. It passes into a well-marked external cingulum which runs around the base of the  $pr^d$  externally and then onto the anteroexternal face, toward the tip of the  $pa^d$ , which it does not quite reach.

The last molar, very rarely preserved in specimens belonging to this family, is here known (U.S.N.M. No. 2693). It is very small, narrower in proportion to its length, and with the cusps lower and less piercing, but otherwise resembles the preceding molars.  $M_6$  is the largest tooth of the molar series.

The molar roots are developed in exactly the same way as in *Dryolestes* and *Laolestes*.

#### MANDIBLE

The characters of the posterior part of the mandible are more completely displayed in U.S.N.M. No. 2693 than in any other mammalian jaw from the American Mesozoic. It agrees very closely with the same parts in the English species of *Amblotherium*. The masseteric fossa is broad and deep. It is not distinctly bounded below, nor anteriorly, where it narrows and debouches onto the external surface of the horizontal ramus, but superiorly it is limited by a strong ridge. This ridge has its origin back of and outside the last molar and it rises and passes into the anterior border of the coronoid. The latter is remarkable, the apex being produced posteriorly into a sharp point directed backward. This point is somewhat crushed and the possibility of its being an artifact was taken into consideration but abandoned. It is quite clearly original and is also seen in the English species. Between this tip and the condyle is a

deep circular notch. The condyle itself is broadly attached and wide transversely. The articular surface faces upward and a little backward and is transversely cylindrical. It is far above the alveolar border. The angular process is much as in other dryolestids, small, styliform, directed backward, continuing the general curve of the lower border.

When both external and internal aspects are taken into consideration, the horizontal ramus is seen to be similar to that of *Laolestes*, although it is relatively more slender. The supposed restriction back of the last molar seems not to be a real original feature of the jaw.

The internal aspect of the jaw is best seen in U.S.N.M. No. 2142. The pterygoid fossa is broad and shallow, bounded below by a moderately developed crest which becomes obsolete as it passes backward toward the angle. The dental foramen is long and oblique and is situated at the anterior corner of the pterygoid fossa. The internal groove begins just anterior to the dental foramen and falls rapidly toward the lower border, reaching it and disappearing beneath  $M_4$ . The symphysis ends posteriorly beneath  $P_1$ .

#### MEASUREMENTS

Lengths:									
	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>	M <sub>5</sub>	M <sub>6</sub>	M <sub>7</sub>
Y.P.M. 11883	0.75	0.7	0.75	0.85	0.85	0.85	..	..	..
U.S.N.M. 2412	0.8	0.8	0.7	0.8	..	..	0.9	..	..
Y.P.M. 13732	..	..	..	..	..	..	0.85	1.0	0.9
Y.P.M. No. 13732: Depth of ramus below M <sub>6</sub>							<div style="display: flex; align-items: center;"> <div style="margin-right: 5px;">{</div> <div style="display: inline-block; text-align: center; vertical-align: middle;"> inside outside </div> </div>	2.0	
								1.2	
U.S.N.M. No. 2693: M <sub>1-8</sub>								5.9	
End of M <sub>8</sub> to tip of angle								7.6	
Top of coronoid to lower border								6.5	

#### *Amblotherium debilis* Simpson 1927

1881. *Dryolestes gracilis*, Marsh, *Amer. Jour. Sci.* (3) XXI, 513.

1927. *Amblotherium debilis*, Simpson, *Amer. Jour. Sci.* (5) XIII, 411.

TYPE.—Y.P.M. No. 11821. Left lower jaw with  $M_{1-6}$  and roots or alveoli of other teeth.

PRINCIPAL REFERRED SPECIMENS.—Y.P.M. No. 13728. Right lower jaw in matrix, outer aspect, with  $M_{1-6}$ .

Y.P.M. No. 13730. Posterior part of right lower jaw, in matrix, inner aspect, with  $M_{5-7}$ . The outer aspect of  $M_{6-7}$  has also been exposed.

Y.P.M. No. 13734 and U.S.N.M. No. 2726 are also referred.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Molars smaller than in *A. gracilis*. External cingulum weaker.  $Pa^d$  slightly lower than  $me^d$  on all molars.  $M_7$  markedly smaller than  $M_6$ .

Marsh's *Dryolestes gracilis* must be referred to *Amblotherium* or "*Stylacodon*" Marsh. It thus becomes a homonym of *Amblotherium gracilis* (*Stylacodon gracilis* Marsh) and a new specific name has necessarily been given it. The distinctions given



in the diagnoses are not thoroughly satisfactory and it is quite probable that some of them will prove to be due to differences of preservation or to individual variation, but it is probable that the species are distinct. The type is badly worn and broken and many of its characters are obscured, but these may be made out with little doubt by comparison with the referred specimens.

## DENTITION

The advanced wear on the type has had the effect of increasing the length of the talonid at the expense of the trigonid, attenuating the cusps, changing their relative heights, etc., so that a casual inspection would seem to warrant generic separation, but this is not confirmed by detailed study. As seen especially in Y.P.M. Nos. 13728 and 13730, the molars agree closely with those of *A. gracilis* but they are somewhat smaller. The talonid is also shorter and narrows more rapidly in passing toward the external side of the tooth. Probably correlated with this is the relatively feeble development of the external cingulum. The paraconid seems somewhat less strong, although this is a character readily modified by even a slight degree of wear.  $M_3$  is apparently the longest tooth of the series, rather than  $M_6$ , although the latter was probably higher, and the disparity in length between  $M_6$  and  $M_7$  is certainly greater than in *A. gracilis*.

## MANDIBLE

The horizontal ramus is stouter in proportion to the very diminutive teeth than in *A. gracilis*. In the type there are apparently three mental foramina, one beneath the anterior root of  $P_1$ , one beneath  $P_2$ , and one beneath the anterior root of  $P_3$ . The other mandibular characters, so far as surely known, are like those of *A. gracilis*.

## MEASUREMENTS

Of all the minute mammals of the American Jurassic, this species is apparently the smallest. The measurements of the type are not very accurate, as the teeth are so worn.

	Lengths:						
	$M_1$	$M_2$	$M_3$	$M_4$	$M_5$	$M_6$	$M_7$
Y.P.M. 11821	0.6	0.6	0.75	0.65	0.5	0.6	..
Y.P.M. 13728	0.65	0.7	0.7	0.65	0.6	0.6	..
Y.P.M. 13730	..	..	..	..	0.7	0.7	0.55
Y.P.M. No. 11821: Depth of ramus below $M_6$	{					inside	1.7
						outside	1.4

*Kepolestes* Simpson 1927

1927. *Kepolestes*, Simpson, *Amer. Jour. Sci.* (5) XIII, 413.

DEFINITION.—Metaconid of molars simple, squarely truncate at end; paraconid curving forward and upward, about as high as metaconid, separated from  $me^d$  by a wide U-shaped notch;  $pa^d$ ,  $me^d$  and talonid cusp in a straight anteroposterior line.

Type species small, but mandible rather closer to that of *Laolestes* than of *Amblotherium*.

TYPE.—*Kepolestes coloradensis* Simpson.

DISTRIBUTION.—Morrison formation, Colorado.

The dinosaur quarries at Garden Park in the southern Colorado foothills yielded three jaws to Professor Marsh's parties. Two are badly preserved docodontids, probably *Docodon* sp. nov., and this is the third. These are of great interest as being the only American Jurassic mammals not from Como Bluff. The present specimen, although imperfect, is also of much interest as presenting what is clearly a new variant of the rather stereotyped dryolestid molar pattern. It is probable that this material is not of exactly the same age as that from Como Bluff, but at present it is not possible to achieve an exact correlation of the various Morrison faunules. The fact that the present genus is not known at the more northern locality may be due to the geographic separation, to slight difference of facies, or (but less probably in view of the large number of specimens from Como Bluff) to accident of collecting. Its generic characters are not such as would indicate a form ancestral to or derived from those just described, and hence it is of no immediate value in exact age determination.

### *Kepolestes coloradensis* Simpson 1927

1927. *K. coloradensis*, Simpson, *Amer. Jour. Sci.* (5) XIII, 413.

TYPE.—U.S.N.M. No. 2723. Right lower jaw in matrix, inner aspect, with  $P_4$  and  $M_{1-8}$ , mostly somewhat broken.

HORIZON AND LOCALITY.—Morrison formation, Garden Park.

DIAGNOSIS.—Sole species of the genus. Total length of molar series *ca.* 6.2 mm.

### DENTITION

Only enough of the last premolar remains to show that it was a high, somewhat recurved tooth about twice as high as the molars. The latter are all of about the same size. The  $me^d$  is blunt, truncated, but not bifid. The paraconid curves forward and upward, leaving a rounded, U-shaped notch between it and the  $me^d$ . On  $M_7$  it rises quite as high as the  $me^d$ , but it was probably a little lower on the preceding teeth. The  $pa^d$  and talonid cusp are in line with the  $me^d$ , as in *Dryolestes* and *Amblotherium*, not slightly internal to it as in *Laolestes*.

### MANDIBLE

The mandible recalls that of *Laolestes* save for its smaller size. The internal groove is much as in other dryolestids, and the symphyseal surface is long and narrow. The alveolar border, in internal aspect, is nearly straight and the lower border forms an evenly convex curve, lowest beneath  $M_6$ .

### MEASUREMENTS

Lengths:						Depth of ramus below $M_6$ , inside
$M_{1-8}$	$M_3$	$M_4$	$M_5$	$M_6$	$M_7$	
<i>ca.</i> 6.2	0.7	0.7	0.7	0.7	0.7	2.2

*Herpetairus* Simpson 1927

1927. *Herpetairus*, Simpson, *Amer. Jour. Sci.* (5) XIII, 413.

DEFINITION.—Dryolestid upper jaws with seven molars, each markedly shorter than broad. Three external marginal cusps on upper molars, the central one largest. Distinct posterior intermediate cuspule, but no other anterior or posterior marginal cusps. Median transverse crest absent or (in a species doubtfully referred) faint. Last premolar with both external and internal cingula, with a single small posteroexternal cingulum cusp.

TYPE.—*Herpetairus arcuatus* (Marsh).

DISTRIBUTION.—Morrison formation, Wyoming.

With this genus begins the description of the Morrison pantothere upper jaws. The type species was referred to *Dryolestes* by Marsh. It probably belongs either to this genus or to *Laolestes*, but it is quite impossible at present to correlate it definitely and therefore, as already explained, a new generic name is provisionally applied to it.

These upper molars are surprisingly different from anything known from later deposits. Each is quite *sui generis*. The correlation of the various cusps with those found in the primitive upper molars of the Cretaceous and Paleocene is an exercise rather in philosophical odontology than in morphology. This is an important task to which the writer hopes to return elsewhere in adequate detail, but as regards probability and permanent value it is of a wholly different order of magnitude from the more sober and fundamental problems set for the present revision. One fact, however, must be insisted upon: these upper teeth are triangular in outline but they are not tritubercular either literally or functionally.

The first tritubercular upper molars known are from the upper Cretaceous. If related at all to the tritubercular type (and the writer believes that they are) these pantotherian upper molars must be adjudged *pretritubercular*. For this reason, and to avoid a premature commitment to theoretical views which might detract from the morphological value of the following descriptions, the terminology of trituberculy is not here used. The cusps are designated chiefly by descriptive phrases—a somewhat clumsy device but apparently the best procedure at present.

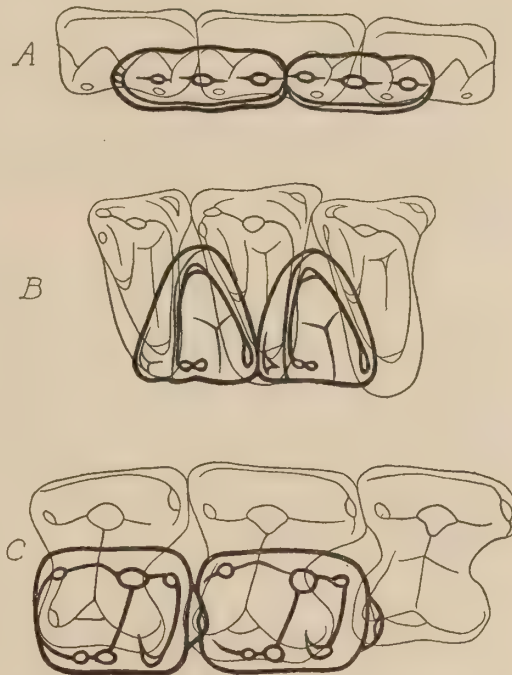


FIG. 27. Diagrams of occlusal relationships in triacodonts and pantotheres. A, *Priacodon*. B, *Laolestes* lower molars and *Herpetairus* upper molars. C, *Docodon*. Lower molars in heavier lines. Not to scale.



Besides the genotype, a second species, ?*Herpetairus humilis*, is doubtfully referred to the genus.

*Herpetairus arcuatus* (Marsh 1879)

1879. *Dryolestes arcuatus*, Marsh, *Amer. Jour. Sci.* (3) XVIII, 397.

1927. *Herpetairus arcuatus*, Simpson, *Amer. Jour. Sci.* (5) XIII, 413.

TYPE.—Y.P.M. No. 11822. Right maxilla with  $M^{2-7}$ , much worn.

NEOTYPE.—Y.P.M. No. 13740. Left maxilla with  $M^{1-4}$ , almost unworn.

REFERRED SPECIMENS.—Y.P.M. No. 13739. Maxilla with  $P^4$  and  $M^{1-3}$ .

Y.P.M. No. 13742. Fragment of maxilla with two molars, provisionally referred.

The following less important specimens are definitely referred to this genus and provisionally to this species:

Y.P.M. Nos. 13741, 13743, 13744, 13746, 13747.

U.S.N.M. Nos. 2724, 2762, 2800, 2818, 2845.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Total length of molar series about 7.5 mm. No transverse median ridge on molars.

DENTITION

Judging from alveoli only, there appear to have been four upper premolars. This number of premolars, both upper and lower, was probably common to all dryolestids. No upper jaw, of whatever genus, is known in which there are surely more than seven upper molars and this number is known to have been definitive for the present genus and some others. Since eight is the normal number of lower molars in the family the heel of  $M_8$  must have been functionless, although it is known to have been retained in *Amblotherium*, at least.

$P^4$  is high, piercing, slightly compressed, conical, not definitely recurved. There is a cingulum, both internal and external. It is weak across the middle of the tooth, but becomes sharp and strong posteriorly, forming a small posteroexternal cuspule. As in the dryolestid lower jaws, the change from premolars to molars is very abrupt. Whatever their history, in this family the premolars and molars retain no definite traces of a common ancestral morphological type nor do the premolars show any tendency toward molarization.

The crown of each molar is obliquely triangular with its anterior border about vertical to a line joining the internal cusps and its posterior border running outward and markedly backward from this line. The width of the teeth<sup>19</sup> increases from  $M^1$  to  $M^5$ , then decreases slightly to  $M^7$ , while the length remains nearly constant to  $M^5$  and then decreases to  $M^7$ . From  $M^1$  to  $M^5$  the teeth thus become relatively narrower, with more acute internal apices, and  $M^{6-7}$  have about the proportions of  $M^5$  but are smaller. The internal cusps are arranged in a nearly straight anteroposterior line, arched very

<sup>19</sup> Throughout this work the term "width" applies to the transverse measurement, regardless of whether it is the larger or smaller dimension.



FIG. 28. *Herpetairus arcuatus*. Right upper molars, crown view, type. Fourteen times natural size.

slightly outward. From the varying widths of the molars it hence results that the outer contour of the series is more strongly arcuate (hence the specific name, which would be equally appropriate for any of the upper jaws here described). It does not follow, as implied by Marsh, that the lower molars were in a similarly arcuate series. Indeed the fact that the lower molars were not arcuate but varied in size and occluded with upper teeth of even more variable size is the apparent mechanical concomitant (whether cause or not) of this arched arrangement.

From these varying proportions and details of arrangement it further follows that the angle between the anterior and outer edges of the molars varies. On  $M^{1-3}$  this angle is over  $90^\circ$ , on  $M^4$  it is about  $90^\circ$ , and on  $M^{5-7}$  it is progressively less than  $90^\circ$ .

Each molar is implanted by three roots, two external and one internal, but the two external roots divide farther and farther from the crown on the more posterior teeth and on  $M^7$  they appear to be confluent, although there are two pulp cavities and the confluent roots are separated by a vertical groove externally.

The internal angle is occupied by a single cusp, the chief apex of the crown, which is high and slender. Like the  $pr^d$  of the lower molars, this cusp is made to seem even more lofty by the fact that the alveolar border is lower on this side of the crown. This internal cusp is crescentic, sending ridges outward along the anterior and posterior borders of the crown. There is an apparent torsion of the tooth which causes this inner portion to point slightly posteriorly.

The outer border of the crown has three cusps. The largest, slightly smaller than the internal cusp, is central and is directly opposite the latter. It is somewhat compressed transversely and sends a sharp low ridge backward to the posteroexternal cusp, and another forward to the anteroexternal one. The latter is anterior and somewhat external to the central cusp. From its apex a distinct and often sharp crest or cingulum runs upward and backward on the outer face of the crown, to end almost directly above the tip of the central cusp. The posteroexternal cusp is of about the same size and is subcrescentic. One wing is formed by the crest running to the centroexternal cusp and one by the crest along the posterior edge of the molar. Along this posterior edge, intermediate between the internal and posteroexternal cusps, is another cuspule which is also subcrescentic. One wing is sharp and is that running along the posterior edge to the posteroexternal cusp, the other is rounded and runs to the internal side of the base

of the centroexternal cusp. This intermediate cusp is always well defined and in some specimens is nearly as large as the centroexternal one.

In exceptionally well-preserved material, such as Y.P.M. No. 13740, it may be seen that the crest from the internal cusp along the anterior edge of the crown runs to the anterior side of the base of the centroexternal cusp, excluding the anteroexternal cusp from the basin of the crown, and that the crest or raised rim along the posterior edge of the crown does not run to the apex of the posteroexternal cusp but terminates in a minute cuspule posterointernal to the latter.

M<sup>7</sup> is known only in a worn condition, but seems to have had the same elements as the other molars. The general crown level is lower and the internal and anteroexternal cusps are larger relative to the other cusps, the latter seemingly being reduced.

In Y.P.M. No. 13742, the anterior limb of the posterior intermediate cusp is sharply crested, rather than rounded.

#### SKULL

The various maxillary fragments referred to this species reveal very little of the cranial osteology. The maxilla is gently incurved above the canine and anterior pre-molar, but posterior to this it is nearly vertical, strong and wall-like. The anterior root of the zygoma is above the last two or three molars. Below this root the alveolar process curves inward around the last molar.

#### MEASUREMENTS

Maximum widths of molars:

	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	M <sup>4</sup>	M <sup>5</sup>	M <sup>6</sup>	M <sup>7</sup>
Y.P.M. 11822	..	1.2	1.5	1.8	1.9	1.8	1.4
Y.P.M. 13740	1.1	1.2	1.4	1.7	..	..	..
Y.P.M. 13739	1.1	1.3	1.6	..	..	..	..
Y.P.M. 13742	..	..	..	1.9	1.9	..	..
Y.P.M. 11822: Length M <sup>2-7</sup>						6.5	
Y.P.M. 13740: Length M <sup>1-4</sup>						5.0	

#### ? *Herpetairus humilis*, new species

TYPE.—Y.P.M. No. 13745, left maxilla with M<sup>3-6</sup>.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Molars with a slight median transverse ridge.

This specimen is of rather doubtful affinities but it cannot be placed in any established species and is of sufficient morphological interest to warrant the application of a name. It resembles *H. arcuatus* in the known features except that a slight rounded ridge is developed in the basin of the crown between the internal and centroexternal cusps. This is perhaps homologous with the median ridge of *Melanodon*, but its development is much less than in that genus.



## MEASUREMENTS

Molar widths:	M <sup>3</sup>	M <sup>4</sup>	M <sup>5</sup>	M <sup>6</sup>
	1.6	1.8	1.9	1.7
Length M <sup>3-6</sup>	4.6			

*Melanodon* Simpson 1927

1927. *Melanodon*, Simpson, *Amer. Jour. Sci.* (5) XIII, 413.

DEFINITION.—Dryolestid upper jaws with seven molars, each markedly shorter than broad. Centroexternal cusp much stronger than in *Herpetairus*, more median, less external. Strong posterior marginal cusp and weak anterior marginal cusp. Strong, sharp median transverse crest. Last premolar without internal cingulum; external cingulum with three cusps—anterior, central, and posterior.

TYPE.—*Melanodon oweni* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

As pointed out by Gregory on the basis of drawings by the present writer, this strongly characterized genus seems to be of peculiar interest from the standpoint of molar evolution (Gregory 1926, fig. 3, III, left hand figure). Two species are recognized, differing in details of molar structure. It is probable that this is the upper dentition either of *Dryolestes* or of *Laolestes*.



FIG. 29. Comparison of upper molars of *Herpetairus* (left) and *Melanodon* (right).

*Melanodon oweni* Simpson 1927

1927. *Melanodon oweni*, Simpson, *Amer. Jour. Sci.* (5) XIII, 413.

TYPE.—Y.P.M. No. 10663. Part of right maxilla with P<sup>4</sup> and M<sup>1-5</sup>.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Centroexternal cusp subconical. Outer border of tooth emarginate opposite this cusp. (A number of lesser differences, see below.)

## DENTITION

The main cusp of P<sup>4</sup> is nearly a true cone, not at all compressed, although it is slightly recurved and has a subtrenchant posterior edge. There is a feeble posteroexternal cingulum, now much obscured, but no true internal cingulum. The external cingulum, on the contrary, is strongly developed, sharp, continuous, and horizontal. It widens and rises in three places to form distinct anteroexternal, centroexternal, and posteroexternal cusps. The arrangement and ground plan of the molars are the same as in *Herpetairus*, but the detailed structure has numerous well defined and important differences.

The raised anterior rim of the basin runs to the centroexternal cusp and up its anterointernal slope to the apex. Halfway between this and the internal cusp it bears a small cusplule, hardly distinguishable on M<sup>2</sup> but progressively stronger until on M<sup>5</sup> it is about half as large as the posterior intermediate cusp. It is not crescentic, but semi-

conical. The anterior face is formed by the vertical anterior shearing edge of the tooth and the posterior face is rounded. There is a prominent and sharp ridge, totally absent in *Herpetairus arcuatus*, running from the internal cusp directly outward across the

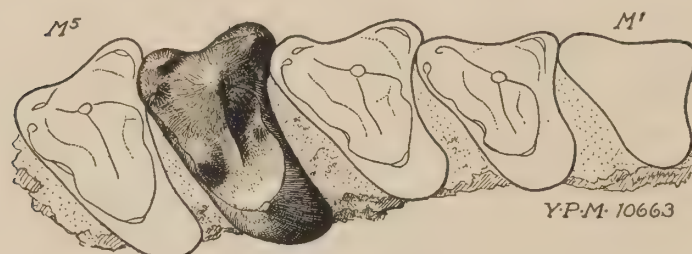


FIG. 30. *Melanodon oweni*. Right upper  $M^{1-5}$ , crown view. Type. Thirteen times natural size.

middle part of the crown to the centroexternal cusp and up the latter to its apex. On  $M^5$  this ridge seems to bear a very slight prominence at the base of the latter cusp. The raised posterior rim of the crown bears a large intermediate cusp, as in *Herpetairus*, but here it is not subcrescentic, but semiconical like the

anterior intermediate cusp just described. It is nearer to the internal cusp and between it and the posteroexternal cusp the sharp basin rim undulates slightly so that there may appear to be one ( $M^2$ ,  $M^5$ ) or two ( $M^{3-4}$ ) tiny cuspules, which would be immediately obliterated by wear. The posteroexternal angle of the crown bears two distinct and nearly equal cuspules. The more posterointernal one marks the end of the posterior crest from the internal cusp and posterior intermediate cusp. The other is connected by a slight anteroexternal ridge to the centroexternal cusp and has also another similar slight ridge external to this which passes onto the base of the centroexternal cusp and quickly disappears. The latter cusp is itself unusually developed. It is quite as high as the internal cusp and rather more bulky. Although nearly conical, three small sharp ridges or angulations, already described, run from its apex, one anterointernally, one directly internally, and one posteroexternally. The anteroexternal angle of the tooth is formed by a small out-jutting cusp, excluded from the rim of the basin. It is crescentic, the concavity posterointernal, facing toward the body of the crown.

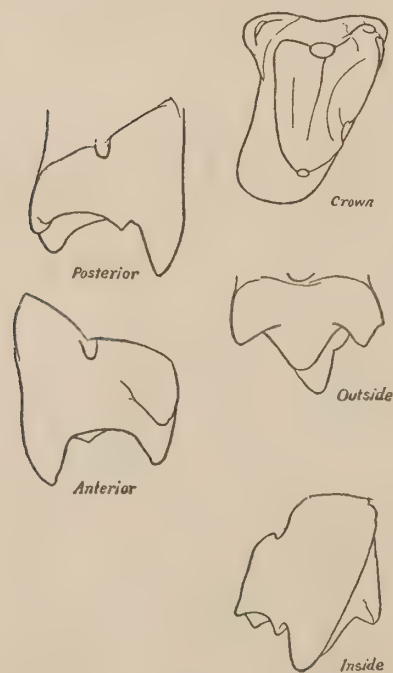


FIG. 31. *Melanodon*. Diagram of typical left upper molar from all aspects.

#### MEASUREMENTS

Widths of molars of type:

$M^2$	$M^3$	$M^4$	$M^5$
1.7	2.0	2.2	2.2
Length $M^{1-5}$			7.3

*Melanodon goodrichi*, new species

TYPE.—Y.P.M. No. 13738. Part of right maxilla with  $M^{3-5}$ .

REFERRED SPECIMEN.—Y.P.M. 13748. Part of right maxilla with  $M^{3-5}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Centroexternal cusp a triangular pyramid, posterointernal face concave. Outer borders of molars straight. (Several lesser differences, see below.)

#### DENTITION

This species is much like the foregoing but differs in a number of details of molar construction. The external border is straight, rather than concave, the anteroexternal and posteroexternal cusps being less external relative to the centroexternal cusp. The latter is slightly smaller relative to the internal cusp and is markedly triangular in horizontal section. The posterior crest from its summit is sharper and runs posterointernally. The posterointernal face is concave rather than convex. The anterior crest from the internal cusp stops at the base of the centroexternal cusp, but a strong angulation runs from the apex of the latter anteriorly toward but not to the anteroexternal cusp. The more posterointernal of the two cusps at the posteroexternal corner of the crown is relatively smaller.

#### MEASUREMENTS

	Widths:			
	$M^3$	$M^4$	$M^5$	Length $M^{3-5}$
Y.P.M. 13738	2.1	2.4	2.4	5.0
Y.P.M. 13748	2.0	2.3	2.3	..

#### *Melanodon cf. goodrichi* Simpson

MATERIAL.—Y.P.M. No. 13749. Right maxilla with  $M^{1-4}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

The teeth of this specimen are smaller than in the type and differ in a few details. The anterior crest from the internal cusp does run to the apex of the centroexternal cusp, so that two distinct angulations, very close to each other, run down the anterior slope of this cusp. The posterior crest from this cusp runs somewhat more externally than in the type of *M. goodrichi*. More material might show this to be a distinct species, but at present it is preferred to impute its peculiarities to individual variation. The molar widths follow:

$M^1$	$M^2$	$M^3$	$M^4$
1.4	1.7	1.9	2.0

#### *Herpetairus* or *Melanodon*, spp. indet.

1880. *Dryolestes obtusus*, Marsh, *Amer. Jour. Sci.* (3) XX, 237.

MATERIAL.—Y.P.M. No. 11819A. Left maxilla with  $P^3$  and  $M^{1-5}$ . Type of *Dryolestes obtusus* Marsh. Fig'd (as *Dryolestes*), Osborn 1904, Pl. XXI, fig. 1A; 1907, fig. 14A.



Y.P.M. No. 10656B. Right maxilla with M<sup>3-0</sup>. Fig'd (as *Dryolestes*), Osborn 1904, Pl. XXI, fig. 1B; 1907, fig. 14B.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

In defining *Dryolestes obtusus*, Professor Marsh gave as distinguishing features the blunt cusps, short crowns, and projection of the last premolar beyond the rest. The first two features are entirely due to wear and corrosion, and the last must have been a misapprehension, for it is not now shown by the specimen. The jaw cannot be identified either generally or specifically and *Dryolestes obtusus* is a *nomen nudum*.<sup>20</sup>

Osborn (1904) later studied both the specimens here under consideration. Unfortunately, at the time of his visit to New Haven the larger part of the material of upper jaws now described for the first time was set aside and had not been cleaned or catalogued. He was consequently obliged to confine himself to this material which is so badly preserved as to be almost wholly uncharacteristic. With the exception of some details which could be visible only to an observer who had access to unworn comparative material, Professor Osborn's figures of these two jaws are very accurate. This lack of comparative material and the impossibility of then appreciating the inadequacy of these specimens, however, inevitably led to some erroneous impressions despite the accuracy of observation. Some of these errors have been adopted into the literature (e.g., by Gregory) and they must be briefly corrected:

1. No known dryolestid upper molars have an internal cingulum. The line here so called is simply the limit to which corrosion has removed the enamel.
2. There are three, not two, external cusps and the highest is central, not anterior.
3. The "external cingulum" noted by Osborn is analogous to the internal one, being the limit of corrosion. There is a sort of cingulum in these upper molars but it is only a ridge running backward from the tip of the anteroexternal cusp for a short distance and it has been entirely removed by wear and corrosion in the present instance.
4. The largest external cusp is not united to the internal cusp by a median ridge in *Herpetairus* but it is in *Melanodon*. It is impossible to say which was the case here.
5. The posterior, not the anterior, ridge is normally stronger and it bears a well marked cusp when unworn.

An inadvertent error in the figure (Osborn 1904, Pl. XXI, fig. 1A) must also be noted. In the palatal view the teeth are correctly labeled, but in the external view "P<sup>4</sup>" should be P<sup>3</sup>; "M<sup>1</sup>," P<sup>4</sup>; "M<sup>2</sup>," M<sup>1</sup>; etc.

The small foramen labeled infraorbital foramen by Osborn is only one of two outlets of the infraorbital canal. The main infraorbital foramen was much larger and was located at the anterior edge of the specimen, directly anterior to this smaller branch, and above the anterior root of P<sup>4</sup>.

The structure of the other specimen available to Osborn is even more obscure. The

<sup>20</sup> There is some slight doubt as to whether Y.P.M. No. 11819a or 10656b is the type of this species. As Marsh left the collection both were together in a small box labeled "*Dryolestes obtusus* (type)." The former is the better specimen, however, and a later manuscript list of types by Marsh seems to put the matter beyond reasonable question. In either event the name is a *nomen nudum*.

enamel is entirely gone and the crowns are reduced to mere shapeless stumps. It has no morphological interest so far as the teeth are concerned, but it does reveal a little of the palate. The choanae were narrow and the posterior end of the palate cuts straight across to them from behind M<sup>7</sup>.

*Euthlastus* Simpson 1927

1927. *Euthlastus*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

DEFINITION.—Pantothere upper jaws, molars more than four and probably seven. Crowns cordiform, with hook-like anteroexternal cusps. Outer border of two rounded lobes separated by median notch, an outer marginal cusp on the anterior lobe, but none on the posterior lobe. Two posterior marginal cusps. Crowns essentially broad basins with raised rims and elevated internal apex. Last three molars broader than long.

TYPE.—*Euthlastus cordiformis* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

*Euthlastus cordiformis* Simpson 1927

1927. *E. cordiformis*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

TYPE.—Y.P.M. No. 13755. Right maxilla with last four molars, all somewhat broken.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Total length of last three molars about 2.2 mm.

DENTITION

The first tooth preserved is too broken to be of much value. It is farther out of the alveoli than the others, no doubt from *post mortem* causes. The last three teeth are alike in essentials. They are cordiform in contour, as the specific name indicates, save for an irregularity due to the projection of the anteroexternal cusp. The point of the heraldic heart outline is internal and is produced into a high, slender, piercing cusp. Its concave external face passes downward into a broad shallow featureless basin which constitutes the whole effective grinding area of the crown. The edge of this basin is sharp and slightly elevated all around it. The outer edge of the external anterior lobe is occupied by a marginal cusp, the internal face of which (toward the basin) is concave. Posterior to this is a marginal notch which separates the outer lobes. The external margin of the posterior

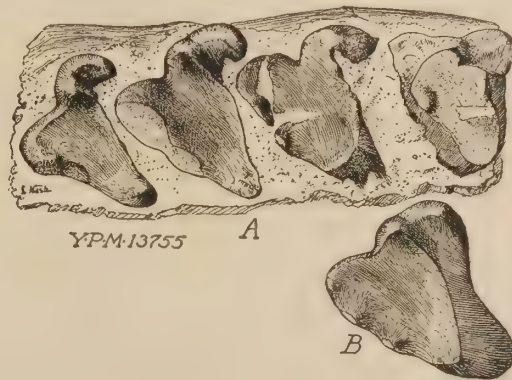


FIG. 32. *Euthlastus cordiformis*. A, last four right upper molars, crown view, type. B, restoration of crown view of upper molar. 25 times natural size.



lobe does not bear a cusp, but there is a small cuspule on its posterior edge. Between this and the internal cusp, on the posterior rim of the basin, is another very small cusp. The anteroexternal cusp projects sharply and is hook-like, as shown in the figures. The last molar is smaller and somewhat more oblique than the other two. The interdental embrasures are exceedingly narrow.

#### MEASUREMENTS

Widths of last three molars: 1.0, 1.0, and 0.9 mm. respectively  
Length of last three molars, together: 2.2 mm.

#### *Miccyloxyrants* Simpson 1927

1927. *Miccyloxyrants*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

DEFINITION.—Pantothere upper jaws with seven molars, the posterior ones, at least, markedly broader than long. Crowns similar to those of *Euthlastus*, but external border straight save for an abrupt median notch on each side of which is an external marginal cusp. A slight rounded transverse median ridge in basin.

TYPE.—*Miccyloxyrants minimus* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

#### *Miccyloxyrants minimus* Simpson 1927

1927. *M. minimus*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

TYPE.—U.S.N.M. No. 2754. Left upper jaw with C, M<sup>4-6</sup>, and alveoli.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Lengths of M<sup>4</sup> to M<sup>6</sup> about 0.7, 0.7, and 0.6 respectively.

#### DENTITION

The canine is a relatively large, simply pointed, recurved tooth implanted by two stout divergent roots. There appears to have been a short diastema and then probably four premolars. Back of this the jaw was broken and turned at an angle before or during burial, so that the cheek tooth formula cannot be certainly determined. There are indications, however, of three molars anterior to those preserved, which, with the three present and one posterior to them, would make seven, probably the correct number. The probable formula is thus I<sup>2</sup> C<sup>1</sup> P<sup>4</sup> M<sup>7</sup>.

The first preserved molar, M<sup>4</sup> by this count, is worn and broken but seems to have differed little from M<sup>5</sup>. The latter is a short broad tooth, not unlike a molar of *Euthlastus* in general aspect but quite different in detail. It is somewhat worn, but the facets of wear are easily delimited. They may mark the destruction of other characteristic features, but they do not mislead with regard to what is original and what secondary on the tooth as preserved. The internal cusp is high, slender, and crescentic, its external face now worn. External to this the crown was shallowly basined, with raised anterior and posterior rims as in *Euthlastus*, but the posterior rim is now truncated hori-



zontally and the anterior rim is obliterated, its place taken by a strongly oblique facet (from wear against the  $pr^d-me^d$  crest of the lower molar). The central part of the basin is occupied by a small but distinct rounded ridge running straight externally from the base of the internal cusp but almost disappearing before reaching the external border. This border would be nearly straight were not its contour broken in the center by a small, abrupt notch. On each side of this notch is a marginal cusp, the posterior one in line with the median transverse ridge, which does not quite reach it. There is a hook-like anteroexternal cusp like that of *Euthlastus*. Along the posterior border there is one marginal cusp somewhat internal to the outer border and, although it is now truncated by wear, there is clear evidence of another, probably larger, posterior marginal cusp between this and the internal cusp.

$M^6$  is a smaller tooth and its external border is more oblique. It was later in eruption, being at a slightly lower level and less worn. The external border is not definitely notched, but is somewhat concave in the center. The anterior of the two centroexternal cusps is prominent, but the posterior one is small. The anteroexternal cusp is relatively broader and less hooked. The raised posterior rim bears one cusp at about its midpoint, but the end of this ridge externally is elevated and is no doubt homologous with the more external posterior cusp of  $M^5$ .

Judging from its apparently confluent alveoli,  $M_7$  was very small.

#### MEASUREMENTS

*Miccyloxyrants* is one of the smallest known mammals.

Length $M^4$	ca. 0.7
Length $M^5$	0.7
Width $M^5$	1.0
Length $M^6$	0.6

#### *Malthacolestes* Simpson 1927

1927. *Malthacolestes*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

DEFINITION.—Pantothere upper jaws. First molar much and second molar a little longer than broad. On these teeth, median transverse crest present, but part of crown anterior to it much reduced and part posterior to it large and basin-like. Interspace between  $M^1$  and  $M^2$  long.

TYPE.—*Malthacolestes osborni* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.



FIG. 33. *Miccyloxyrants minimus*. Left  $M^{5-6}$ . Type. A, crown view. B, external view. 25 times natural size.

*Malthacolestes osborni* Simpson 1927

1927. *M. osborni*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

TYPE.—Y.P.M. No. 13751. Part of right maxilla with  $M^{1-2}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Lengths of first two molars each about 1.3 mm.

## DENTITION

$M^1$  is very narrow, being only slightly over half as wide as the following tooth although about as long. The structure shows some analogy with that of *Melanodon*, but the differences are so marked that this may be misleading. There is a main internal cusp as before, but the anterior crest has apparently been lost, or at least is not present, and the same is consequently true of the basin or depression which is seen between this crest and the median transverse crest in *Melanodon*. The posterior division of the



FIG. 34. *Malthacolestes osborni*. Right  $M^{1-2}$ , crown view, type. 22 times natural size.

crown, between the median transverse crest and the posterior rim, is, on the contrary, well developed and elongated. The centroexternal and internal cusps are approximated in this very narrow tooth so that their bases are confluent. The former is considerably the lower, is compressed transversely, and sends a sharp ridge to the posteroexternal cusp. The latter, the extra cuspule postero-internal to it, and the posterior marginal cusp are all present and distinct. The anteroexternal cusp was apparently well developed, but it is broken.

$M^2$  partakes of the peculiarities of  $M^1$  but is somewhat closer to *Melanodon*. There is a very faint anterior crest on the internal cusp, but it does not reach the centroexternal cusp and does not inclose a true basin between itself and the median transverse ridge. The internal and centroexternal cusps are farther apart and are connected by a sharp ridge. There is no anterior ridge or angulation on the centroexternal cusp. The posterior half of the crown is much like that of  $M^1$  save for its greater transverse width.

## MEASUREMENTS

Width $M^1$	0.7
Length $M^1$	ca. 1.3
Width $M^2$	1.1
Length $M^2$	1.3

*Pelicopsis* Simpson 1927

1927. *Pelicopsis*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

DEFINITION.—Pantothere upper jaws. Antepenultimate molar longer than broad, penultimate about as broad as long, and last molar broader than long. Crowns basined,

with raised margins bearing, aside from the hook-like anteroexternal heel which is excluded from the basin, a marginal, ridge-like anteroexternal cusp and one median cusp on the posterior margin. Posteroexternal angle raised slightly but not truly cusp-like.

TYPE.—*Pelicipsis dubius* Simpson.

DISTRIBUTION.—Morrison formation, Wyoming.

*Pelicipsis dubius* Simpson 1927

1927. *P. dubius*, Simpson, *Amer. Jour. Sci.* (5) XIII, 414.

TYPE.—Y.P.M. No. 13754. Right maxilla with last three molars.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Sole species of the genus. Lengths of last three molars 1.3, 1.3, and 0.8 mm. respectively.

#### DENTITION

From the proportions of the teeth preserved, it seems probable that this genus had less than seven molars, possibly only four or five. From this fact and from the shape of the interdental embrasures it is unlikely that it is a dryolestid and it is not improbable that it is a paurodontid.

The antepenultimate molar is a stout tooth, its crown slightly longer than broad. The internal cusp is broken, but it was by far the largest and highest cusp of the tooth. The top of the crown is a broad shallow basin with the rim raised all around it. The anterior rim is a crest running straight externally from the anterior limb of the subcrescentic internal cusp. Near the external border it rises to form a ridge-like cusp, presumably the homologue of the centroexternal cusp in *Herpetairus* and *Melanodon* but much less pronounced than in those genera, and it then curves posteriorly and is continued in the external rim of the basin. The posteroexternal angle is slightly raised, but there is no true cusp here. On the posterior border, however, about halfway to the internal cusp, is a cusp-like rising of the elevated rim. The anteroexternal cusp is excluded from the basin and has the usual rather heel-like form, but it is not so hooked as in *Euthlastus*, for example, or as in the more posterior molars of this same specimen.

The penultimate molar differs only slightly from the foregoing. It is broader, but of about the same length. The anteroexternal cusp of the elevated rim is less prominent. There is a faint trace of a median ridge in the basin at the base of the internal cusp. The outer surface of the anteroexternal heel is more hemispherical and its apex is pushed slightly inward and is more hook-like.



FIG. 35. *Pelicipsis dubius*. Last three right upper molars, crown view, type. 25 times natural size.



The last molar is about as broad as the preceding one and is much shorter. As usual for last molars, its obliquity is in the opposite direction from that of the preceding tooth. The raised edges of the basin do not bear any distinct cusps and there is a distinct but low and rounded ridge running down the otherwise concave external face of the internal cusp, but this ridge does not cross the basin. The anteroexternal heel is very distinctive, accentuating the hook-like apex and smooth, hemispherical external surface seen on the preceding molar.

## MEASUREMENTS

	Length	Width
Antepenultimate M	1.3	1.1
Penultimate M	1.3	1.4
Last M	0.8	1.3

*Docodontidae*, new name

1887. *Diplocynodontidae*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 338.

1888. *Dicrocynodontidae*, Osborn, *Am. Nat.*, XXII, 1078.

DEFINITION.—Upper and lower molars subquadrate, complicated by the presence of cusps not seen in other known pantotheres. Lower molars supported by two subequal roots and with relatively large basined heels with two talonid cusps. Nine (?) to twelve cheek teeth.

TYPE.—*Docodon* Marsh.

DISTRIBUTION.—Upper Jurassic, England and North America.

This family includes the most peculiar and highly modified of the pantotheres. Their molars are much the most complicated dental structures known from the Jurassic or, indeed, with the possible exception of some of the Cretaceous multituberculates, from the entire Mesozoic. This peculiarity was recognized by Marsh who in 1887 created for them the distinct family "*Diplocynodontidae*." Osborn at first (1888A) referred Marsh's genera to the *Amphitheriidae*, but this was based on erroneous conceptions both of *Amphitherium* and of the docodontids and was soon corrected by Osborn himself. No subsequent doubt has been cast upon the unity of the group and its right to separation from all other pantotheres.

Some doubts have, indeed, been cast on the right of the *Docodontidae* to inclusion in the *Pantotheria*, although such a position is usually accepted. Gidley (1906, p. 105), in accordance with his known extreme polyphyletic conception of mammalian evolution, stated that the molars of "*Dicrocynodon*" were apparently derived from the simple reptilian cone independently of the molars of *Dryolestes*,—a view which would logically lead to placing this genus in an order, subclass, or even class distinct from that to which the other pantotheres are referred. As this was based on the most exact knowledge of docodontid molar structure hitherto attained, it is worthy of consideration, although further analysis seems to disprove it beyond any question. Gregory (1922, p. 59-60) stated that he had failed to find a solution of the problem of occlusion

between the upper and lower molars of this type and, without doubting the propriety of referring the lower molars to the Pantotheria, he thus left the true nature and relationships of the family in the gravest doubt.

We are now fortunately in a position to answer all the questions clearly raised by Gidley and by Gregory. Not the slightest suspicion can attach to the association of the upper and lower jaws as originally proposed by Marsh and supported by Gidley. By actual trial it was possible to find two specimens, one of the upper and one of the lower dentition, which fitted together almost as if they had come from one individual. The occlusal relationships are thus clearly revealed and are brought out in the accompanying figure. (Fig. 27.)

Returning on this basis to the question of relationships to the other, more normal, pantotheres, detailed study reveals an underlying agreement imperfectly masked by a great but superficial dissimilarity. All of the original pantothere cusps, as seen, for instance, in *Dryolestes* and *Melanodon*, are present and they retain their original relationships, both to their fellow cusps of the same tooth and to those of the occluding teeth. Superposed on this clear original pantotherian inheritance, which leaves no valid basis for Gidley's view of independent origin, there is a specialization, confusing but not really profound. No new crests are developed and no cusps are lost. All that has happened is a modification of the proportions of the molars, broadening of the basins and strengthening of the cusps, and the addition of one small new cusp in the upper molars and of three small new cusps in the lower molars. The result appears very bizarre to eyes accustomed to the repertoire of Tertiary molar specialization, not because it is more profound, but because it departed from a more primitive basis and did not exactly follow any of the lines of evolution illustrated in later mammals. It must be regarded as a premature and ill fated effort toward the production of broad-crowned crushing or grinding teeth from the more ancient piercing insectivorous type.

The mandibular features are in exact agreement with this view. All the characters of the *Amphitherium* mandible are present, slightly modified, and on them are superimposed some peculiar but superficial specializations.

Since the above passage was first written, it has received important confirmation by the discovery in the English upper Jurassic of a docodontid which approaches the other pantotheres more nearly in molar structure than does *Docodon* itself. This genus, *Peraiocynodon* (Simpson 1928B, p. 125), is a true member of the Docodontidae, with the specialized lower molar heel and other characters of the family, but it retains a narrower and more triangular trigonid with three main cusps. This trigonid is intermediate in character between that of *Amphitherium* or *Peramus* and that of *Docodon*, although somewhat closer to the latter.

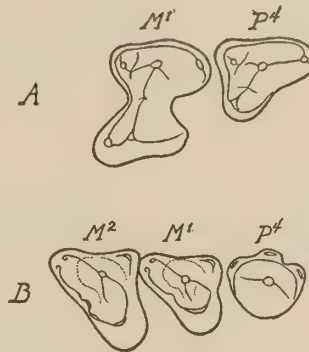


FIG. 36. Premolar-molar transition in pantothere upper teeth. A, *Docodon*. B, *Melanodon*.



Marsh described three genera, *Diplocynodon* = *Dicrocynodon* = *Diacynodon*, *Docodon*, and *Enneodon* = *Ennacodon*. If valid, these would now be called *Dicrocynodon*, *Docodon*, and *Ennacodon*, and they have generally been accepted under these names. In his former studies (e.g., 1927B, p. 415-6) the present writer has followed custom in recognizing all three genera, although he has already pointed out that they are almost surely synonymous. He now feels, however, that this practice cannot reasonably be continued. As will immediately be shown, separation of the genera cannot be maintained and the continued recognition of all three names, even provisionally, would perpetuate an incorrect name not only for the most characteristic and perfect specimens but also as the name of this peculiar and important family. The step was not previously taken because of reluctance to modify nomenclature so long established, but the change appears to be inevitable and can better be made in the present detailed revision than in some future and possibly more obscure paper.

#### *Docodon* Marsh 1881

1880. *Diplocynodon*, Marsh, *Amer. Jour. Sci.* (3) XX, 235. Non *Diplocynodon*, Pomel, 1846.  
 1881. *Docodon*, Marsh, *Amer. Jour. Sci.* (3) XXI, 512.  
 1887. *Enneodon*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 339. Non *Enneodon*, Heckel, 1853, non *Enneodon* Prangner, 1845.  
 1888. *Dicrocynodon*, Marsh in Osborn, *Jour. Acad. Nat. Sci. Phila.* (2) IX, 263. To replace *Diplocynodon*, preoccupied.  
 1890. *Ennacodon*, Marsh, Additional genera, etc., 15. To replace *Enneodon*, preoccupied.  
 1890. *Diacynodon*, Schlosser, *Biolog. Centralbl.*, X, 242. To replace *Diplocynodon*, preoccupied. Antedated by *Dicrocynodon*.

DEFINITION.—Dental formula  $I_{3+}^1 C_1^1 P_{3-4}^3 M_{7-8}^{6+?}$ . Lower molars subquadrate. Trigonid about as wide as talonid; in addition to main external cusp with a prominent anteroexternal cusp, two well-developed internal cusps, and low anterointernal basined cingulum.

TYPE.—*Docodon striatus* Marsh.

TYPES OF SYNONYMS.—*Dicrocynodon victor* (Marsh). *Ennacodon crassus* (Marsh).

DISTRIBUTION.—Morrison formation, Wyoming and Colorado.

This genus is usually referred to in recent texts and papers as *Diplocynodon* or *Dicrocynodon*. There is no justification for the continued use of the former name, which properly belongs to a well-known genus of Crocodilia. *Dicrocynodon* is not preoccupied, but evidence is here adduced to show that this name is synonymous with the earlier *Docodon*.

In defining *Docodon*, the only generic difference from "*Diplocynodon*" given by Marsh was that it had but seven molars, while "*Diplocynodon*" had eight. The dental foramen was supposed to be farther forward, but other characters were admitted to be in close agreement. Close simultaneous comparison of the two types, both of which are excellent specimens, confirms the difference in molar number, but fails to reveal any



other difference, however slight. These jaws and teeth are the most complicated known from the Jurassic and it seems inconceivable that two such well-known and complex forms could really belong to two different genera differing in no slightest detail save in the possession of seven or of eight molars. The slight variations in measurements are



FIG. 37. *Docodon*. Diagrammatic internal view of right lower jaw.  
Three times natural size.

within the probable limits of error in taking such minute dimensions. The teeth agree not only cusp for cusp but even, on the molars, in the fine details of the furrows and rugosities on the enamel. In view of the known facts of dental embryology and variation it is quite impossible to maintain the two genera as distinct. The apparent absence of  $M_8$  in *Docodon striatus* might be interpreted in three ways: (1) as due solely to the youth of the type, (2) as an individual anomaly, such as is not infrequent in other mammalian groups, or (3) as a taxonomic distinction of not more than specific value. The type is young, but careful dissection of the posterior portion failed to reveal the germ of an additional tooth. It seems more probable that the variation in molar number is an anomaly, perhaps the more likely in these mammals with seven or eight similar molars, but for the present it seems best to retain Marsh's species provisionally. *Docodon striatus* rests on a single specimen which had not quite reached maturity. An analogous case is seen in *Amblotherium*, in which the molar number is usually eight, also, but is seven in one individual specimen and nine in another.

"*Enneodon*" (*Ennacodon*) was defined as having a comparatively short, robust jaw with nine post-canine teeth, all of the same type, and with  $P_2$  larger than  $P_1$  rather than smaller as in *Docodon* and *Dicrocynodon*. Two species were defined, each based on a single, immature specimen. Measurements show that the jaws in these species are shorter than in the others referred to the family but that they are more slender, both absolutely and relatively to the size of the teeth. Both differences in proportion could be due to immaturity. The post-canine teeth do appear to number nine, although this is in part based on the number of alveoli and is a little doubtful. The statement that the premolars and molars are of the same general form was based on study of the teeth when half concealed by matrix. Upon being cleaned somewhat the premolars and

molars prove to be entirely distinct in pattern. There were three erupted premolars and apparently six erupted molars. Gathering together all the specimens which show the premolars clearly (Fig. 38), one sees at once that the premolar distinction of the sup-



FIG. 38. *Docodon*. Diagrams of lower premolars in nine different specimens, to show variability of  $P_2$ . B is younger than the others and is Marsh's *Ennacodon*.  $H^1$  is a diagrammatic superior view showing the crowding of  $P_{3-4}$  in H.

posed genus *Ennacodon* is not that  $P_2$  is larger than  $P_1$  but that the homologue of  $P_2$  of the other forms is absent. With these changes in interpretation the differences for which one must account are as follows:

*Docodon*

1. Premolars four.
2. Molars seven or eight.
3. First molar somewhat smaller.
4. External premolar cingula strong.
5. Mandible stouter and longer.

*Ennacodon*

1. P<sub>2</sub> lacking.
2. Molars apparently six.
3. First molar somewhat larger relatively than in *Docodon*.
4. External premolar cingula weaker.
5. Mandible more slender and shorter.

Great as these differences appear, none is of generic value. (1) Study of a rather extensive series of specimens shows that in these forms P<sub>2</sub> is erupted later than P<sub>1</sub> and P<sub>3-4</sub>. Whether it is of the second or first dentition is not clear—so far as has been observed its late appearance is not connected with the late disappearance of a predecessor. It is a small tooth and may be in process of disappearance. Its apparent absence in *Ennacodon* could be due entirely to the youth of these two specimens. This is supported by the existence of another, hitherto unmentioned, specimen which has P<sub>2</sub> but which cannot otherwise be separated from *Ennacodon crassus*. (2) The lower molar number may then be due to the same cause, immaturity. Some jaws of this group have six erupted molars, some seven, and some eight, and those with six or seven have other signs of youth. (3) The apparent slight difference in the relative size of M<sub>1</sub> may be illusory and in any event is of not more than specific value. (4) The same is true of the slight apparent difference in the development of the premolar cingula. (5) The different proportions of the jaw are such as always exist between younger and older individuals of the same species. There are other unimportant differences which serve to separate the two species *Ennacodon crassus* and *Ennacodon affinis* but are not common to the two in distinction from *Docodon*. It is impossible reasonably to maintain that *Ennacodon* and *Docodon* are separate genera. The species are retained and are referred to *Docodon*. They do have some slight differences from the other species now referred to this genus, but these are so unimportant, and even doubtful, that their real validity can only be tested by a still larger series of specimens than is now available. It is probable that *Docodon* includes more than one species, and perhaps as many as four or five, but one must hesitate to vouch for the necessary validity of all of the present established species.

Like those of the other pantotheres, the upper jaws referable to this family have not been found in actual association with the lowers. Nevertheless we are relieved of the necessity for creating a special genus for them by the placing of all the lower jaws in a single genus. There is no question, as pointed out above, that these upper jaws do belong in this family and they clearly can be placed in the one American genus, *Docodon*. It is now impossible, however, to separate the upper jaws into species or to place them in one or another of the four species based on lower jaws. They are therefore placed provisionally in a distinct species, *Docodon superus*, to serve for purposes of description and reference until association can be demonstrated.



*Docodon victor* (Marsh 1880)

1880. *Diplocynodon victor*, Marsh, *Amer. Jour. Sci.* (3) XX, 235.

1888. *Dicrocynodon (victor)*, Marsh in Osborn, *Jour. Ac. Nat. Sci. Phila.*, IX, 263.

TYPE.—Y.P.M. No. 11826. Right lower jaw nearly complete, with C, P<sub>1-4</sub>, and M<sub>1-6</sub>. Fig'd, Marsh 1887, Pl. X, fig. 3; Lull 1917, Pl. XVI.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Cheek teeth P<sub>4</sub> M<sub>8</sub>. M<sub>7</sub> slightly larger than M<sub>7</sub> of *D. striatus*. M<sub>1-2</sub> slightly smaller than M<sub>1-2</sub> of *D. crassus* or *D. affinis*. Mandible somewhat longer and deeper than in the other supposed species.

## DENTITION

The incisors are not known, but from alveoli they numbered at least three and possibly four, and they were arranged in an anteroposterior series as in the dryolestids.

The canine is a large tooth, higher than any which follow, and implanted by two separate roots, the anterior a little smaller and more nearly vertical. The tip is recurved, pointing backward and inward, the anterior margin convex, the posterior concave in lateral profile. There is a small heel. The tooth is not unlike that of *Laolestes*.

The four premolars are similar save in size and some minute details. Each has a single trenchant, somewhat elongate main cusp, its sharp point directed slightly backward and also inward. On the posterior slope of this cusp is an accessory cusp, less strongly marked on the anterior than on the posterior premolars. In the type of this species it is worn off on P<sub>1</sub>. There is also a smaller anterior accessory cusp, somewhat higher on the crown, and also less marked on the more anterior teeth. Each premolar has a prominent, sharp, continuous internal cingulum. This runs around the posterior end of the tooth, forming a small posterior heel or cingulum cusp or, as on P<sub>4</sub> of the type, two distinct small cusps, one posterointernal and one posteroexternal. On P<sub>3-4</sub>, at least, the cingulum passes onto the external face and then forward and upward, becoming obsolete before reaching the middle of the crown. On P<sub>4</sub> the cingulum may also run around the anterior end of the tooth, forming a small anteroexternal cusp, and onto the external face. The external cingulum is always interrupted in the middle, however.

P<sub>2</sub>, contrary to the almost universal rule, is smaller than P<sub>1</sub>. It is apparently in process of reduction and does not appear until the other premolars are already in place. P<sub>3</sub> and P<sub>4</sub> in this species are of almost the same size, although P<sub>3</sub> may be a trifle shorter and more slender. Both are larger than P<sub>1</sub>.

Each molar has seven distinct cusps, each with its own size, shape, and invariable relationships to the other cusps. M<sub>5-6</sub> are the largest and most typical and they may be described first. The contour, as seen from above, is not triangular as in other pantotheres but rectangular, about one and one-half times as long as broad, with rounded corners. The outer face is convex, save for a shallow vertical median groove, and rises to a high, slightly recurved external cusp, slightly anterior to the midline. This is the largest cusp on the tooth and is undoubtedly the protoconid. About halfway up its

anterior slope it bears a stout but much smaller cusp which, by comparison with the more primitive *Peraiocynodon*, appears to be the homologue of the paraconid, more external here than in other pantotheres. Also along the outer border, but lower and more separate from the  $pr^d$  is the external talonid cusp. It has the position of the hypoconid of later mammals. The internal face of the tooth is also convex and bears a similar row of marginal cusps. The highest of these is a little posterior to the midline and only about half as high as the  $pr^d$ . It appears to be the  $me^d$ . On its posterior slope, only a little lower than it and hardly smaller, is the internal talonid cusp. This has about the position of the talonid cusp of the dryolestids and may be homologous, although this is not quite certain. The conditions in *Peraiocynodon* suggest that the external talonid cusp of the docodontids is more probably the original pantothere talonid cusp which has here moved relatively externally from its original median position (*Amphitherium*) while it moved relatively internally in the dryolestids. Anterior to the  $me^d$  is a more distinctly separate cusp of about half its height. In *Docodon* this anteroexternal cusp looks like the paraconid, but again *Peraiocynodon*, which differs but little from *Amphitherium* or *Peramus* in the trigonid, offers a more probable homology. This anteroexternal cusp in *Peraiocynodon* is just appearing, is, indeed, hardly visible, and is rather clearly a new structure while the anteroexternal cusp is the paraconid. As might be expected, comparison of the highly specialized *Docodon* with the differently specialized dryolestids gives different results from comparison of the more primitive *Peraiocynodon* with the ancient and most primitive *Amphitherium*.

The  $me^d$  and  $pr^d$  are connected across the middle of the tooth by a stout, oblique transverse ridge. Posterior to this ridge is a basin which constitutes about half of the crown and is clearly a basined talonid. It is open posteriorly or, more correctly, is closed posteriorly by the anterior end of the following molar.

From near the apex of the anteroexternal cusp ( $?pa^d$ ) there runs outward and downward on the anterior face of the crown a cingulum which widens and forms a small, low cusp anterior to the main anterointernal cusp. There are thus seven cusps, three of which have no homologues in the dryolestids.<sup>21</sup>

Besides the cusps and the main transverse ridge there is a complicated pattern of lesser furrows and ridges. These are not, as might be supposed, random or variable features but are quite invariable throughout the genus, even including the species hitherto placed in distinct genera. From the notch between the  $pr^d$  and anteroexternal cusp a furrow runs straight inward to end at the external side of the base of the anterointernal cusp. Another, ending at the same point, runs down the anterointernal face of the  $pr^d$  from near its apex. Also from near the apex of the  $pr^d$  a furrow runs straight inward to the notch between the  $me^d$  and anterointernal cusp. The talonid is marked



FIG. 39. *Docodon*. Crown view of typical right lower molar. Fifteen times natural size.

<sup>21</sup> The anterointernal cingulum cusp has an analogue and possible homologue in *Peramus*, but not in other known pantotheres.



by two curved transverse furrows, one running from the notch between  $pr^d$  and  $me^d$  on the main transverse ridge down into the basin and up to the notch between the  $pr^d$  and the posteroexternal cusp, and the other from the notch between the  $me^d$  and the postero-internal cusp into the basin and up the internal slope of the posteroexternal cusp. Three grooves run from near the tip of the  $pr^d$  posteriorly and a little internally until they meet the first of the transverse talonid furrows. The minor features of this pattern are quickly obliterated by wear, but at least traces of the pattern can always be seen.

Anterior to  $M_5$  the molars become progressively narrower relative to their length and also decrease slightly in absolute height and length.  $M_{7-8}$  were progressively smaller than  $M_{5-6}$ . The most anterior molars are so narrow that the internal cusps appear much like so many elevations of an internal cingulum plastered on the higher external cusps.

#### MANDIBLE

The horizontal ramus is slender, the alveolar border nearly straight, the lower border gently convex, with its greatest depth below  $M_5$ . The single mental foramen is beneath the anterior root of  $P_3$ . The symphysis is not very clear in this species, but seems to have extended back as far as the last premolar. Coronoid, condylar, and angular processes are distinct and well marked.<sup>22</sup> The former is large, high, and long. Its edges are not thickened and it is flat and plate-like. Anteriorly it arises at an angle of about  $60^\circ$  to the alveolar border, and it originally extended back as far as does the condyle, from which it was separated by a small notch. The latter is pedunculate and is somewhat lower than in *Laolestes*. The articular surface looks backward and but little upward and is slightly elongate transversely.

The external face of the jaw back of the alveolar portion is slightly excavated, but there is no distinct masseteric fossa. A slight convexity passes posteriorly to the condyle. The angular process, below this, is concave externally, but its lower border is thickened. The internal aspect of this region is like that of *D. striatus*, where it is more clearly displayed.

#### MEASUREMENTS OF TYPE

Lengths:

C	$P_1$	$P_2$	$P_3$	$P_4$	$M_1$	$M_2$	$M_3$	$M_4$	$M_5$	$M_6$
1.5	0.9	0.8	1.2	1.3	1.4	1.7	2.0	2.1	2.1	2.0

Depth of ramus below  $M_4$ , inside, 4.1 mm.

<sup>22</sup> Since it was studied by Marsh and before the present research the type mandible was removed from the matrix. The posterior portion was cracked in many places before this, and in clearing it the pieces were all retained, but their relationships very slightly altered. By carefully washing the surface and checking against a good X-ray photograph it has been possible to avoid erroneous impressions from this source, but these changes should be kept in mind in studying photographs. The coronoid now appears too slender and low, the supracondylar notch too large, and the curvature of the horizontal ramus too great (due to a median break repaired with plaster some of which remains between the two broken surfaces).



*Docodon striatus* Marsh 1881

1881. *Docodon striatus*, Marsh, *Amer. Jour. Sci* (3) XXI, 512.

TYPE.—Y.P.M. No. 11823. Right lower jaw in matrix, internal aspect, with C, P<sub>1-4</sub>, and M<sub>1-5</sub>. Fig'd, Marsh 1887, Pl. X, fig. 2.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Cheek teeth apparently P<sub>4</sub> M<sub>7</sub>. M<sub>7</sub> slightly smaller than that of *D. victor*. M<sub>1-2</sub> slightly smaller and jaw longer and stouter than in *D. crassus* or *D. affinis*.

## DENTITION

The whole dentition is hardly distinguishable from that of *D. victor*. P<sub>1-2</sub> seem slightly larger, but they are worn in the type of *D. victor*. The internal cingula on P<sub>3-4</sub> are slightly straighter, but the difference might be individual. The molars, so far as preserved, agree in every detail. M<sub>5</sub>, preserved in both, is of the same size. Judging from alveoli, this was also true of M<sub>6</sub>, but M<sub>7</sub> was smaller in the present species. Dissection of the jaw seems to indicate that there was no M<sub>8</sub>, even when adult, a point which has been sufficiently discussed above.

## MANDIBLE

The internal features of the mandible are also like those of *D. victor*, but they are here more clearly displayed. The symphysis is unusually long, ending beneath the first or second molar. The condyle was broken off (previous to the preparation of the earliest figure) and refixed at a slightly incorrect angle, so that at first sight it appears quite different from that of *D. victor*, but this was not original. From the condyle there runs forward a ridge which is very high and sharp just anterior to the neck of the condylar process and above the posterior end of the angle. It here has its outer edge turned upward, undoubtedly for the attachment of one or both of the pterygoid muscles. Anterior to this it becomes lower and more rounded and passes into the alveolar border behind the last molar. Beneath this ridge and debouching posteriorly at the upper part of the condylo-angular notch there is a wide and deep groove. It becomes more shallow, without narrowing, as it passes forward, and then becomes deeper again and communicates with the dental foramen. Below this groove is a ridge which runs forward and passes into the lower part of the alveolar portion of the mandible, and below this is the somewhat convex inner surface of the effected angle.

Anteriorly the internal groove is a normal, narrow, rather deep sulcus, nearly reaching the symphysis and diverging slowly from the lower border and broadening as one follows it posteriorly. Beneath the anterior end of M<sub>7</sub> it branches, the upper narrower branch running back to a point just anterior to the dental foramen, and the lower broader main branch passing onto the ridge immediately above the angle, where it becomes shallower and disappears at a point considerably posterior to the dental foramen and below it.

The bone of the horizontal ramus is marked by numerous striations above and

below the internal groove, a fact which suggested the specific name. This resembles the similar condition in the bone of most very young mammals and no doubt is due to the same cause.

## MEASUREMENTS OF TYPE

Lengths: C	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>	M <sub>5</sub>
ca. 1.3	1.0	0.8	1.2	1.2	1.5	1.8	1.9	2.0	2.0

Depth of ramus below M<sub>4</sub>, inside: 3.9 mm.

*Docodon crassus* (Marsh 1887)

1887. *Enneodon crassus*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 339.

1889. *Ennacodon (crassus)*, Marsh, Additional genera, etc., 15.

TYPE.—U.S.N.M. No. 2130. Right lower jaw in matrix, outer aspect, with C, P<sub>3-4</sub>, and M<sub>1-4</sub>. Fig'd (as *Enneodon crassus*), Marsh 1887, Pl. X, fig. 4.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Cheek teeth apparently P<sub>3</sub> M<sub>6</sub>, but probably P<sub>4</sub> M<sub>7-8</sub> in adult. Jaw shorter and more shallow, but this probably also due to youth. M<sub>1</sub> apparently larger than in *D. victor* or *D. striatus* and posteroexternal premolar cingula less developed, ending weakly and indefinitely anteriorly. P<sub>3</sub> = P<sub>4</sub>.

## DENTITION

Save for the details mentioned in the diagnosis, the dentition is like that of *D. victor* or *D. striatus*. The posterior portion of the jaw is now so broken that it cannot be restored, but according to Marsh there were alveoli for two additional molars, making six. But there is no assurance that more were not still enclosed in their crypts.

## MANDIBLE

Except for its youth and the crushing which it has suffered, the mandible does not differ in the known parts from that of the preceding species.

## MEASUREMENTS OF TYPE

Lengths: C	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>
1.6	1.4	1.4	1.8	1.9	2.0	2.1

Depth of ramus below M<sub>4</sub>, outside: 3.2 mm.

*Docodon affinis* (Marsh 1887)

1887. *Enneodon affinis*, Marsh, *Amer. Jour. Sci.* (3) XXXIII, 339.

1889. *Ennacodon (affinis)*, Marsh, Additional genera, etc., 15.

TYPE.—U.S.N.M. No. 2129. Left lower jaw in matrix, outer aspect, with C, P<sub>1</sub>, P<sub>3-4</sub>, and M<sub>2-4</sub>.

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—Cheek teeth apparently P<sub>3</sub> M<sub>6</sub>, but individual probably immature. Proportions of jaw nearly as in *D. crassus*. M<sub>1</sub> apparently larger than in *D. victor* or

*D. striatus*. Canine smaller than in *D. crassus*. Possibly a small diastema.  $P_4$  larger than  $P_3$ . Premolar cingulum with a minute median external cuspule.

There are so many trivial distinctions between this species and the other three that it may well be valid, although no one of its supposed characteristics can be relied upon as certain and as of definite taxonomic value. Marsh separated it from *D. crassus* as having a less robust lower jaw, more slender canine, and a small post-canine diastema.

#### DENTITION

The canine is a little smaller than in the preceding species, but is otherwise identical. The space back of it is broken and disarranged in the specimen, so that it is not certain whether the supposed small diastema really existed or not. The alveoli clearly indicate six molars, as stated by Marsh, but do not preclude the possible presence of others not yet erupted.

#### MANDIBLE

There are mental foramina beneath  $P_1$  and  $P_2$ . The masseteric fossa is well developed, but not sharply bounded. The coronoid arises at a lower angle than in *D. victor* or *D. striatus*, possibly another youthful character.

#### MEASUREMENTS OF TYPE

Lengths:	C	$P_1$	$P_3$	$P_4$	$M_1$	$M_2$	$M_3$	$M_4$
	1.4	1.1	1.3	1.5	..	2.0	2.0	..

Depth of ramus below  $M_4$ , outside: 3.1 mm.

#### *Docodon superus*, new species

TYPE.—Y.P.M. No. 10647. Right maxilla with canine and  $M^{1-5}$ .

PRINCIPAL REFERRED SPECIMENS.—Y.P.M. No. 13769. Left maxilla with C,  $P^{1-3}$ ,  $M^{1-2}$ , and an isolated molar.

Y.P.M. No. 13770. Right maxilla with  $P^3$  and  $M^{2-4}$ .

U.S.N.M. No. 2715. Right maxilla with  $P^1$ ,  $P^3$ , and  $M^{2-5}$ .

HORIZON AND LOCALITY.—Morrison formation, Quarry 9, Como Bluff, Wyoming.

DIAGNOSIS.—A conventional species for upper jaws of this genus. Maximum lengths of first five molars of type 1.8, 1.9, 2.0, 1.9, 1.6 mm. respectively.

#### DENTITION

The canine is a large high tooth, slightly recurved, implanted by two stout roots. The anterior face is convex in contour and is apparently trenchant, but posteriorly there is a concave face, making the tooth triangular in section.

No specimen indicates the presence of more than three upper premolars. This may indicate that another was late in eruption, as in the lower jaws, but it is more probable that reduction had gone farther than in the lowers and that three was the definitive number.  $P^1$  is very small, follows the canine immediately, and has only one root. It has a trenchant but stout main cusp and a small sharp internal cingulum rising to a



tiny cusp near the middle of the internal face. A curving ridge runs down the internal face to this cuspule from the apex of the crown.  $P^2$  is larger, has two roots, and has a small posterior accessory cusp but otherwise closely resembles  $P^1$ .

$P^3$  exhibits the same general features—a main trenchant cusp with posterior accessory cusp, an internal cingulum, here very strong, rising to form a marked high cusp just posterior to the middle of the tooth on its internal face, a small anterior cingulum cusp, and a ridge running down from the apex of the main cusp to the internal cusp. In this tooth the latter is also followed by a small posterior accessory cusp. This genus is the only one known from the Jurassic in which there is really any close comparison between the last upper premolar and the first molar. (See Fig. 36.)  $P^3$  has all the elements of  $M^1$  and they are arranged in the same way. Nevertheless there is a definite break between the two series.  $P^3$  is much smaller than  $M^1$ , its external cusps are without furrows, its internal cusps relatively smaller, the anterior basin less developed, etc. It is, however, unique among Jurassic mammals in that it is patently becoming molariform and that its parts are severally homologous with those of the molars.<sup>23</sup>

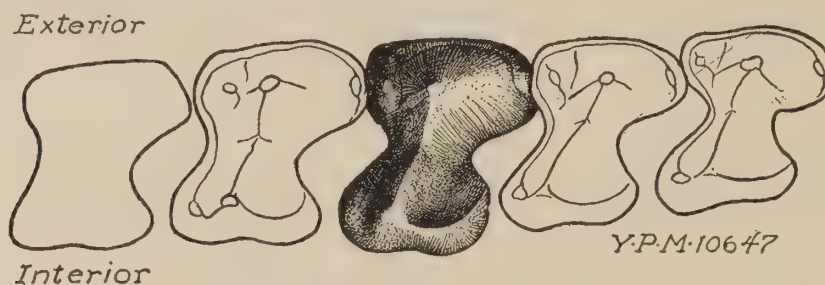


FIG. 40. *Docodon superus*. Right  $M^{1-5}$ , crown view, type.  $12\frac{1}{2}$  times natural size.

The pattern is the same for all the molars save for differences in proportions.  $M^3$  is the largest and least oblique. Anterior to it the molars are narrower anteriorly than posteriorly and posterior to it the reverse is the case. The crown of  $M^3$  may be thought of as divided into two parts, one external and one internal. The external part consists chiefly of one large cusp, the highest and strongest on the tooth, which is sharply pointed and compressed transversely but not truly trenchant. Posterior to it is an accessory cusp of about half its height. Both of these are skirted externally by a sharp cingulum which rises anterior to the main cusp to form a distinct basal cingulum cusp.

<sup>23</sup> The belief is current that mammals were primitively homodont, within the Class as such, and that the Jurassic mammals had departed but little from this condition, having a graded series with slow transition from  $P^1$  to the last molar. How false the supposed evidence drawn from the Jurassic forms has been, should already be evident to the reader and hardly needs emphasis. Having in mind the characters of the order Pantotheria as a whole, it seems justifiable to say that the incipient molarization of  $P^3$  in *Docodon* is one of its numerous specializations, and not a primitive feature retained by this genus and lost by all other pantotheres. The subject, however, more properly belongs in a treatment of molar evolution than here.

On quite unworn teeth a minute posterior external cingulum cusp may also be seen. The internal part of the crown has one main cusp opposite and somewhat posterior to the main external cusp and not over two-thirds as high as the latter. This internal cusp points somewhat backward and it sends a crest forward which curves slightly externally and forms one side of a very deep basin—a basin, however, which is open anteriorly, save for the preceding tooth. Posterior to the centrointernal cusp is another cusp, somewhat lower and on the slope of the larger one. The main internal and external cusps are united by a strong and somewhat oblique transverse crest, sinking to a low notch or saddle between the cusps. A less prominent ridge parallels this one posterior to it, running externally from the posterointernal cusp. Just internal to the posteroexternal cusp, this ridge divides, one branch skirting the external cusps posteriorly and continuous with the external cingulum, the other running up the internal slope of the posteroexternal cusp. The internal face of the main external cusp is furrowed, several furrows passing anterointernally and one posterointernally. The external face of this cusp is also marked by an irregular but distinct series of vertical furrows or wrinkles.

Two rather small circular roots support the external portion of each molar and a large tapering triangular root supports the internal half.

#### SKULL

*Docodon* apparently had a rather long and slender snout, slightly constricted back of the canine. The infraorbital canal is long, opening just above the posterior root of P<sup>2</sup> and anterior root of P<sup>3</sup>. The zygoma arises external to M<sup>5</sup>.

#### MEASUREMENTS

	C	P <sup>1</sup>	P <sup>2</sup>	P <sup>3</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	M <sup>4</sup>	M <sup>5</sup>	
Y.P.M. 10647	{ ..	..	..	..	1.8	2.2	2.4	2.3	2.0	Widths
	{ 1.8	..	..	..	1.8	1.9	2.0	1.9	1.6	Lengths
Y.P.M. 13769	1.7	0.8	1.0	1.3	1.7	..	..	..	..	Lengths
Y.P.M. 13770	{ ..	..	..	1.1	..	2.2	..	..	..	Widths
	{ ..	..	..	1.3	..	1.9	..	..	..	Lengths

## B. MAMMALS OF THE UPPER CRETACEOUS FORMATIONS

In North America mammals have so far been derived from three Cretaceous horizons, the Belly River of Alberta, the Edmonton of Alberta, and the Lance of Wyoming and its equivalents in Montana and South Dakota. Perhaps the best single specimens are those from the Belly River, but they are very few in number and do not give a good knowledge of the fauna as such. Only two very dubious single teeth have so far been found in the Edmonton. The chief mammalian fauna is that of the Lance and its equivalents. Some thousands of separate specimens are known, but this apparently well-



represented fauna is in fact very inadequately known. The specimens consist for the most part of isolated teeth which cannot be associated into natural genera in the majority of cases. A few fragments of jaws are known, but even these are inadequate for the solution of many of the more detailed problems of taxonomy. The attempted revision of the upper Cretaceous faunas is thus on quite a different basis from that of the Jurassic fauna. With the latter, whatever its imperfections, one is at least dealing for the most part with jaws with their included teeth and direct comparisons between the established genera are possible in most cases, but in dealing with the Cretaceous mammals even the characters of two consecutive teeth of a single genus cannot be determined in many instances.

The history of our knowledge of the faunas has also added difficulties. This knowledge is chiefly due to O. C. Marsh and H. F. Osborn. These two workers approached the problem from diametrically opposed viewpoints. As the fragmentary Lance collections came to him, Professor Marsh proceeded to name and publish them on an analytical basis, that is, he applied names not necessarily to distinct animals but to different types of teeth. Under the circumstances there was much to be said for this procedure. Admitting its artificial nature, yet it would have given an adequate nomenclature which would have served as an admirable basis for later revision if it could have been carried out systematically. In practice, the method broke down, indeed its apparent basis of analysis was perhaps not formally recognized. The number of different tooth types became so great, that Marsh felt forced to attempt synthesis in some cases, that is, to refer different types of teeth to one genus or to one species on the grounds that they possibly were different parts of the same type of dentition. Marsh himself thus recognized the impracticability in this case of what we must perceive to have been his fundamental approach, but the inadequate data at hand for synthesis made correct association in the limited genera which he had established impossible and his attempts at such association thus led rather to further confusion than to clarity, although this was due to nature of the material.

Marsh's work was done rapidly, as the material came in, lot by lot, from the field with the expressed hope that rapid publication and illustration would compensate for the errors which Marsh himself knew to be inevitable under these circumstances. Professor Osborn, with Marsh's work before him, attempted a synthetic revision. His aim was to abandon any attempt to give a distinct name to each distinct type of tooth and instead to give names only to whole animals, that is to reconstitute the dentitions scattered parts of which had been given different names by Marsh in many cases. This method, while simpler and giving more enduring results, also had its shortcomings. In order to make it workable at all, the modern conception of genus and of species could not be applied. Thus it is evident that the material referred by Osborn to *Ptilodus* includes many species which would be seen to be quite distinct were good jaws or complete dentitions of each available, or even if the whole taxonomy were based on the variations in homologous teeth,  $P_4$  or  $M^1$  for example. But in attempting to base a taxonomy on *all* the material, including isolated teeth from all parts of the dentition,



the lack of association absolutely prevents the definition of useful species which are even distantly comparable in scope to the species of other and better known mammalian faunas.

The condition is not much changed today. Knowledge of later, related mammals has increased greatly and given greater scope for the employment of analogy, but it is still impossible to reconstitute the entire dentition of even one genus. Thus the same primary problems which faced Marsh and Osborn face the present attempt. It is clear that a revision, in the strictest sense, is impossible. One can only bring the earlier conceptions more into line with the advanced knowledge and methods of today; one cannot establish a detailed taxonomy comparable to those lately established for many of the Tertiary faunas. In attempting even this much one must again make a choice between analysis and synthesis. Should one revive all of Marsh's names and propose the very numerous new names which would be necessary for a thorough analysis of tooth types, or should one follow Osborn in essentials and use generic names for agglomerations of different forms which can be separated, in various parts of the dentition, from other similar agglomerations but which must be much more comprehensive than the genera of any other fauna?

After due consideration, the latter course has been adopted, with such exceptions as are forced by proper respect for the rules of nomenclature. Many of Marsh's generic names and perhaps the majority of his specific names are thus neither recognized as valid and used nor definitely reduced to synonymy. They are simply *included* in other genera or species which are used in a very broad sense. In the case of genera based on isolated teeth, no serious attempt is made to distinguish species beyond the necessary recognition of one species as a genotype. Separation of such genera into species is impossible and unnecessary at present.

The main result of this work is hence not an actual systematic revision of the upper Cretaceous mammals, but a broader treatment which nevertheless permits one to gain an adequate and important conception of the general character of the fauna and of the range of morphological variation exhibited by its different groups.

Three orders occur: Multituberculata, Marsupialia, and Insectivora—the most ancient of all mammalian orders and the most primitive orders of the two great groups of modern mammals.<sup>24</sup> The several faunas are essentially one for morphological purposes as there are no clear differences due to age or facies, and they are treated together. Separate faunal lists are given in a later section of this work. The fragments from the probable Cretaceous of Patagonia are also included.

The following treatment, especially of the multituberculates, follows Osborn's revision of 1893 in many of the broader essentials. There are, of course, numerous differences both in morphological conceptions and, particularly, in views as to affinities, but the credit for the first fundamental approach toward the solution of the broader problems (many of them, however, even now not completely solved) is Osborn's.

<sup>24</sup> Aside, of course, from the monotremes, the pre-Pleistocene history of which is at present totally unknown.

## ORDER MULTITUBERCULATA

Cope 1884

SUBORDER *PLAGIAULACOIDEA* Simpson 1925

This order and suborder have been defined above. All of the upper Cretaceous multituberculates are apparently referable to the single family Ptilodontidae.

## PTILODONTIDAE Simpson 1927

DEFINITION.—Dental formula  $\frac{2}{1} \frac{0}{0} \frac{3-4}{1-2} \frac{2}{2}$ . Enlarged incisors rooted, with extra-alveolar portion almost completely enameled or with restricted enamel band extending (in youth) into the alveolus.  $P_3$ , when present, small, one-rooted, fitting into a notch in  $P_4$ .  $P_4$  large, laterally compressed, trenchant, with serrate edge and lateral ridges. Anterior upper premolars not opposed by lower teeth, grasping, with three to six conical cusps. Only the last upper premolar shearing in function, enlarged.  $M^1$  with three cusp rows, the inner usually incomplete anteriorly;  $M^2$  with three cusp rows, the outer always incomplete posteriorly. Molar cusps more or less crescentic. Wear not reducing molar surfaces to planes but accentuating longitudinal ridges and grooves. First molars much larger than second. Skull triangular as seen from above. Animals usually of small size relative to Taeniolabididae.

TYPE.—*Ptilodus* Cope. (Paleocene.)

DISTRIBUTION.—Upper Cretaceous of Mongolia and North America. Paleocene of Europe and North America. Eocene of North America.

This is the largest and best known of all multituberculate families. So far as present records show, its greatest development was in the Paleocene when it was probably world-wide,<sup>25</sup> but in North America, at least, it survived into the true Eocene (*Encosmodon ultimus* Granger and Simpson, 1928) and the upper Cretaceous multituberculates cannot be excluded from it. *Cimolomys* certainly belongs here, but some of the other forms, such as *Meniscoëssus* and *Djadochtatherium* are more provisionally referred.

*Paronychodon* Cope 1876

1876. *Paronychodon*, Cope, *Proc. Ac. Nat. Sci. Phila.*, 1876, 256.

DEFINITION.—With compressed, grooved lower incisors like those of *Meniscoëssus*.

TYPE.—*P. lacustris* Cope.

<sup>25</sup> It is not known from Africa or from South America, but no mammal-bearing Paleocene deposits are as yet known in either continent. The Polydolopids are not multituberculates and the fauna in which they occur, the so-called *Notostylops* fauna, is almost surely of middle or upper Eocene age.

As was noted by Osborn (1893, p. 313), the single specimen on which this genus rests is not separable from *Meniscoëssus*. If synonymy were proven, *Paronychodon* would become the correct name of the genus, but there is so much doubt as to the age and relationships of this single specimen that the matter of synonymy must be left in abeyance for the present.

*Paronychodon lacustris* Cope 1876

1876. *P. lacustris*, Cope, *Proc. Ac. Nat. Sci. Phila.*, 1876, 256.

TYPE.—Amer. Mus. No. 3970 (*Cat. Fossil Reptiles*). Isolated lower incisor.

HORIZON AND LOCALITY.—From the Judith River region, Montana. Said by Cope to be from the Fort Union, probably Hell Creek.

DIAGNOSIS.—Sole species now referred to genus. Material inadequate.

This was actually the first Cretaceous mammal to be described, but its true character could not then be appreciated and it was referred to the Dinosauria. Not until Osborn's work of 1893, after numerous other Cretaceous mammals were known, was its mammalian nature recognized. The age is doubtful, but it is probably from the Hell Creek beds, the Lance equivalent. This would be in keeping with its probable synonymy with *Meniscoëssus*. Although said to be from the Judith River, it was apparently not derived from the Judith River beds. These were known to Cope, and the present specimen was referred not to them but to the higher "Fort Union," which then included the Hell Creek in this area.

*Meniscoëssus* Cope 1882

1882. *Meniscoëssus*, Cope, *Am. Nat.*, XVI, 830.

DEFINITION.—Lower incisor deep, strongly compressed laterally, with enameled crown, strongly grooved on inner and outer faces.  $P_3$  present.  $P_4$  relatively short and high, with not over nine serrations. Molar cusps very strongly crescentic.  $M_2$  elongate. Doubtfully associated posterior upper premolars short, high, with four or five cusps in main series and a single supplementary external basal cusp. Jaws relatively short and robust. Species larger than those of *Cimolomys*.

TYPE.—*M. conquistus* Cope.

DISTRIBUTION.—Lance formation, Wyoming, South Dakota. Hell Creek beds, Montana.

INCLUDED GENERA

1889. *Dipriodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 85. Type: *D. robustus* Marsh.

1889. *Tripriodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 86. Type: *T. coelatus* Marsh.

1889. *Selenacodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 86. Type: *S. fragilis* Marsh.

1889. *Halodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 87. Type: *H. sculptus* Marsh.

1889. *Oracodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 178. Type: *O. anceps* Marsh. Doubtfully included.



The status of this generic name, as here used, was sharply challenged by Marsh who pointed out that among the original specimens of Cope was a dinosaur tooth which was included in the definition. Osborn, however, accepted the name on grounds which seem to be valid and it is the one now in common use. It is true that the genus was based on three specimens, a mammalian  $M^2$ , an ankylosaurid dinosaur tooth, and the distal end of a mammalian humerus, but the mammal tooth was clearly considered as the type and the name should be taken as applying to it alone. The humerus fragment probably does belong to *Meniscoëssus* also.

*Meniscoëssus*, *sensu lato*, shows relatively little variation in homologous parts of the dentition and includes either a single natural genus or at most two very closely related genera. The original specimen seems to be unique in some respects and the name *Meniscoëssus conquistus* is limited to it. The Montana specimens probably belong to a single species and differ slightly from the South Dakota or Wyoming material. They may hence be included in a distinct species which has been called *Meniscoëssus borealis*. The Wyoming specimens probably include several species, but these cannot be usefully separated at present and all are included in *M. robustus*, *sens. lat.*, at present, using the first trivial name applied to a specimen from this region.

*Meniscoëssus conquistus* Cope 1882

1882. *M. conquistus*, Cope, *Am. Nat.*, XVI, 830.

TYPE.—Amer. Mus. No. 3011.  $M^2$ , broken. Fig'd, Cope 1884, fig. 7.

HORIZON AND LOCALITY.—"Laramie" (i.e., Lance equivalent), South Dakota.

DIAGNOSIS.—Outer cusp row of  $M^2$  with at least four distinct cusps and nearly as long as the median row. First cusp of inner row not well separated from second. Width 5.8 mm., estimated length about 6.6 mm.

*Meniscoëssus borealis* Simpson 1927

1927. *M. borealis*, Simpson, *Amer. Mus. Novitates*, No. 267, 3.

TYPE.—Amer. Mus. No. 14411. Isolated  $M^2$  left.

HORIZON AND LOCALITY.—Hell Creek beds, near head of Crooked Creek, Dawson County, Montana.

DIAGNOSIS.—Cusp formula of  $M^2$  4:4:5, first cusp of inner row more distinct from second than in *M. conquistus*, measuring 8.3 mm. in length by 7.0 mm. in width.

In addition to the type,  $M^1$ ,  $I^2$ ,  $I_1$ , and  $P_4$  are known at least in part. They agree in general with those of *M. robustus*, below.  $M^2$  is considerably larger than in *M. conquistus* and is slightly larger and distinctly more elongate than in *M. robustus*.

*Meniscoëssus robustus* (Marsh 1889)

1889. *Dipriodon robustus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 84.

TYPE.—Y.P.M. No. 11234. Isolated  $M_2$  right. Fig'd, Marsh 1889A, Pl. II, figs. 13-15.

HORIZON AND LOCALITY.—Lance formation, Niobrara County,<sup>26</sup> Wyoming.

DIAGNOSIS.— $M_2$  cusp formula 4:2, length 7.7 mm., width 5.2 mm.  $M^2$  (referred, type of "*Tripriodon coelatus*"), cusp formula 3:3:4 or 3:4:4, length 6.6 mm., width 6.4 mm. Species used in a broad sense for all *Meniscoëssus* from the Niobrara County Lance.

#### INCLUDED SPECIES

1889. *Dipriodon lunatus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 85. Type: Y.P.M. No. 11825, isolated  $M_1$ . Fig'd, Marsh 1889A, Pl. II, figs. 16-18.
1889. *Tripriodon coelatus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 86. Type: Y.P.M. No. 11853, isolated  $M^2$ . Fig'd, Marsh 1889A, Pl. II, figs. 19-21.
1889. *Tripriodon caperatus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 86. Type: Y.P.M. No. 11852, isolated lower incisor. Fig'd, Marsh 1889A, Pl. III, figs. 18-20.
1889. *Selenacodon fragilis*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 86. Type: Y.P.M. No. 11897, fragment of isolated  $M^1$ . Fig'd, Marsh 1889A, Pl. II, figs. 22-24.
1889. *Selenacodon brevis*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 177. Type: Y.P.M. No. 11876, isolated  $M^2$ . Fig'd, Marsh 1889B, Pl. VII, figs. 9-12.
1889. *Halodon sculptus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 87. Type: Y.P.M. No. 11810, isolated  $P_4$ . Fig'd, Marsh 1889A, Pl. III, figs. 11-13.
1889. *Oracodon anceps*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 178. Type: Y.P.M. No. 11862, isolated last upper premolar. Fig'd, Marsh 1889B, Pl. VIII, figs. 13-16. Doubtfully included.
1892. *Oracodon conulus*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 256. Type: U.S.N.M. No. 2141, isolated last upper premolar. Fig'd, Marsh 1892A, Pl. VII, fig. 8. Doubtfully included.

For convenience a list is given of Marsh's figures of specimens now included in this broad species:

- Marsh 1889A, Pl. II: Figs. 13-24.  
 Pl. III: Figs. 1-22.  
 1889B, Pl. VII: Figs. 5-12.  
 Pl. VIII: Figs. 1-3, 13-16.  
 1892A, Pl. V: Figs. 1-7.  
 Pl. VI: Figs. 1, 5.  
 Pl. VII: Figs. 6-8.

Apparently two, possibly more, species are present, but they are clearly closely related. Marsh's generic types are principally based on different parts of the dentition. Only close comparison with the better known *Ptilodus* makes their association in one genus possible.

#### DENTITION

LOWER INCISORS.—Y.P.M. No. 11852 (*Tripriodon caperatus*) is typical of the

<sup>26</sup> "Laramie of Converse County"—the formation is now known as Lance (a restricted part of the old Laramie) and the localities are in what is now Niobrara County. For exact localities of all these forms see Lull, 1915A.

lower incisors of this genus. Its association is confirmed by the fact that it fits the alveolus of a good specimen (Y.P.M. No. 10613) with much of the lower jaw intact, including  $P_{3-4}$  and  $M_1$ . The crown is pointed and saber-like, the median surface flat where it was appressed against its fellow, the outer surface convex. The enamel covers the entire

crown but ends abruptly at the mouth of the alveolus. It is marked by a number of grooves and ridges radiating from the tip. The root tapers to a point beneath the anterior end of  $M_1$  and contains a large pulp cavity which ends anteriorly at about the beginning of the true crown.

**LOWER PREMOLARS.**—The specimen mentioned above, Y.P.M. No. 10613, contains both lower premolars. They are preceded by a wide diastema.  $P_3$  is much reduced, one-rooted, pillar-like, its tip inserted in a notch beneath the overhanging anterior part of  $P_4$ . It is very similar to that of *Ptilodus*.  $P_4$ , in this jaw, is of the shearing type so well known from the Paleocene members of the family. The cutting edge is semicircular and had apparently nine serrations, although these cannot be counted posteriorly. There are eight oblique ridges on the lateral faces of the crown. Y.P.M. No. 11810 (*Halodon sculptus*) is similar to the above but is slightly shorter relative to its height and has coarser striations. It may represent a distinct species. Comparable teeth are common in the collections and generally show nine projections on the shear-

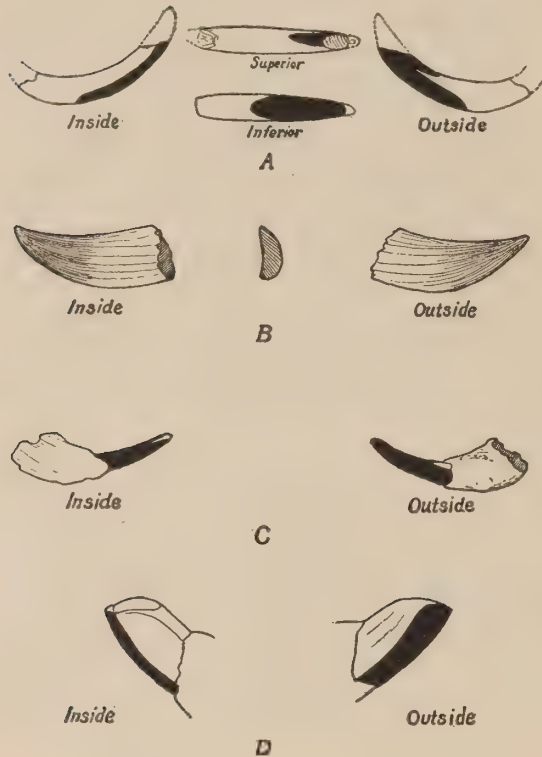


FIG. 41. Multituberculates. Lower incisors. A, *Ctenacodon*. B, *Meniscoessus*. C, *Cimolomys*. D, *Taeniolabis*. B is completely enamel covered. The enamel is solid black in the other drawings. A transverse section of B is given. Not to scale.

ing edge and seven or eight distinct lateral ridges, the posterior ones rather faint. One specimen, at least, appears to have only eight serrations. The teeth may at once be distinguished from those referred to *Cimolomys* by their larger size, shorter and higher proportions, and relatively small number of serrations.

**LOWER MOLARS.**—Y.P.M. No. 11825 (*Dipriodon lunatus*) is Marsh's type  $M_1$ . As is commonly true in multituberculates, it is narrower than any referred  $M_2$ , measuring 4.1 mm. in width and 8.7 mm. in length. The cusp formula is 5:4.<sup>27</sup> The structure is quite simple for a ptilodontid. Each cusp is strongly crescentic, the crescents

<sup>27</sup> That is, five cusps in the outer row, four in the inner. The outer row is mentioned first, the middle row, if present, next, and the inner row last in giving cusp formulae for multituberculates.



opening backward, and all are of about the same size save the reduced anteroexternal cusp. They are not arranged in pairs transversely.

Several variants, perhaps representing as many species, are known. Thus in Y.P.M. No. 10608 the small anteroexternal cusp is almost vestigial and there is a similar minute cusp at the posterior end of the same row. In Y.P.M. No. 10614 the cusps are more nearly opposite transversely.

M<sub>2</sub> is well seen in Y.P.M. No. 11234, the type of the species.<sup>28</sup> This specimen measures 7.7 mm. in length and 5.5 mm. in width and has a cusp formula of 4:2. The first three of the external cusps are subequal, the last a little smaller. The outer slope of each external cusp is conical and the inner slope is produced into a sharp crest curving inward and backward. The anterior of the two inner cusps is crescentic, opening backward, and is larger than any of the outer cusps. The posterointernal cusp is of about the same size and is more nearly conical, although two crests run backward and a little outward on its external slope. The longitudinal midgroove is marked by antero-posterior motion of the opposing row of cusps. It is deep and V-shaped. The bases of all the cusps are marked by small rugations in the midgroove. The crown ends squarely in front, but the posterior border is at an angle of about 45° to the long axis, the outer row being longer than the inner. The coronoid process arises external to this tooth and the alveolar border ends abruptly posterior to it.

UPPER INCISORS.—It is impossible to say whether I<sup>1</sup> was present. It was already very small in the Jurassic. I<sup>2</sup> was certainly correctly identified by Osborn and had also been correctly associated by Marsh with his *Halodon*, which is included in this genus. The median surface is slightly concave, the outer broadly convex. The tip is bifid, the two sharp points being so arranged as to make the tip somewhat spatulate, or with an approach to a transverse chisel-edge, but this is not produced nor accentuated by wear against the lower incisors, which are sharply pointed. About halfway up the high crown on its posterior side is another sharp cusp. The extra-alveolar part of the tooth is completely covered with a thick coat of enamel, which does not extend down into the alveolus. In life the tooth was apparently very slightly procumbent.

I<sup>3</sup> is apparently represented by similar teeth, but they are smaller, with lower crowns, the tip single. A posterior accessory cusp is present as on I<sup>2</sup>.

UPPER PREMOLARS.—Speaking of the upper premolars of *Meniscoëssus*, Osborn says (1893, p. 319), "No teeth are found which can with certainty be considered the upper premolars of *Meniscoëssus*; we naturally look for something similar to the upper premolars of *Ptilodus*, and we find it represented most nearly in the types *Oracodon anceps* and *O. conulus* Marsh." This the present writer considers correct, with not much greater uncertainty than attends the whole process of reconstructing an animal by patchwork. There are about a dozen good specimens similar to Marsh's *Oracodon* in the Yale Collection, and a few more in the American and National Museums. None of these is small enough to pertain the *Cimolomys*, sens. lat., they are just the length

<sup>28</sup> This last right lower molar was considered as the last left upper molar by Marsh. Working before the group was adequately known, Marsh was inevitably led into a number of similar misidentifications. It has not seemed necessary to correct them all formally here; all are corrected by implication.

of the abraded surface of  $P_4$  in *Meniscoëssus*, they represent a modification of the type seen in other ptilodontid genera, and each is strongly worn on one side with fine oblique striae due to shearing. They are, however, peculiar in detail and rather unlike the homologous teeth in any other genera. Each of their several cusps is conical,

pointed, with light crenulations radiating from the apex. In the type of *Oracodon anceps* (Y.P.M. No. 11862) the main tip is eroded and the tooth is not as satisfactory as in a referred specimen which resembles it closely. In this tooth, Y.P.M. No. 10378, the crown rises to an eccentric apex which, from analogy with later genera, is probably posterior. In a row anterior to this point and rapidly decreasing progressively in height are three other cusps. External to the second of these is a small cusp of about the same size as the anterior cusp of the main row. There is a cuspule of like size posterointernal to the apex, and another smaller one postero-external to this point. Other specimens differ chiefly in size. *O. conulus* is larger and has an additional cuspule posterior to the main point. These teeth are shorter relative to  $M^1$  than in *Ctenacodon* or *Ptilodus*, but the same is true of  $P_4$  relative to  $M_1$ . Furthermore it is probable that the last upper premolar was shorter than the last lower premolar, as is generally true in the Multituberculata.

Granted that these teeth, *Oracodon*, represent the last upper premolar of *Meniscoëssus* there remains the question as to whether other upper premolars occurred.

In this connection it is important to remember (1) that all other multituberculates with lower premolars like those of *Meniscoëssus*, some of them with the lower premolars still more reduced, have three or four upper premolars, (2) that the only genus known to have but one upper premolar (*Taeniolabis*) has the most reduced  $P_4$  in the order and is a very different adaptive type from *Meniscoëssus*, and (3) that *Meniscoëssus* is apparently closely related to its contemporary *Cimolomys* and but little more specialized, and *Cimolomys* is known to have had at least four premolars. *A priori* then, one would expect *Meniscoëssus* to have at least three upper premolars and possibly more.

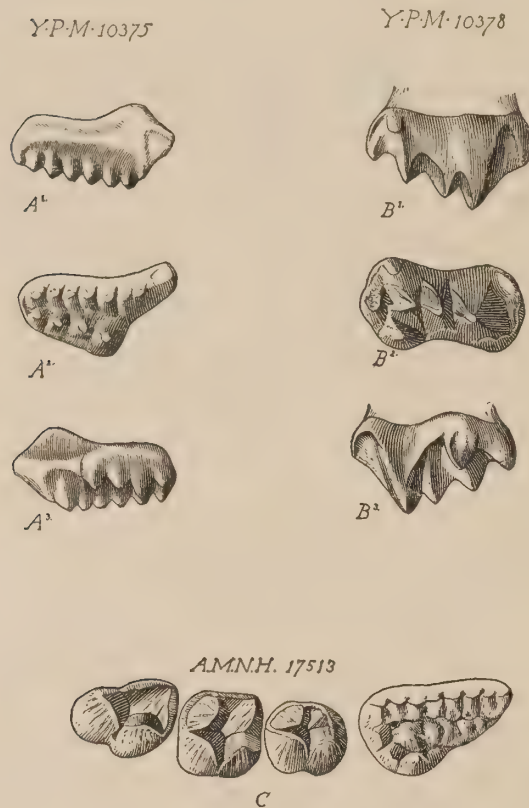


FIG. 42. Multituberculates. Upper premolars. A, *Cimolomys*, internal, crown, and external views of last upper premolar. B, *Meniscoëssus* ("Oracodon"), internal, crown, and external views of last upper premolar. C, *Ptilodus*, crown view of upper premolars.



The larger of the anterior premolar teeth in the Yale collection were carefully measured and their ratios to the lengths of  $M^1$  and  $M^2$  calculated for *Meniscoëssus* and *Cimolomys* in an effort to determine whether they might belong to the larger genus. The figures established for these genera and the comparative ratios for earlier and later allies need not be repeated here, but the results may be briefly put in words. The figures show that even the largest anterior upper premolars in the collections would be smaller relative to the molars of *Meniscoëssus* than are these teeth in *Ptilodus* or in *Ctenacodon*. On the other hand they are considerably too large to have belonged to even the largest species of *Cimolomys*, and they are no smaller relative to the molars of *Meniscoëssus* than is the probable last upper premolar of this genus. The results are not conclusive, but they point with considerable probability to the presence in *Meniscoëssus* of upper premolars in addition to the last one. These were reduced in size, and possibly also in number, and their true arrangement is entirely unknown.

UPPER MOLARS.—*Selenacodon fragilis* is based on  $M^1$  of *Meniscoëssus*, but the type (Y.P.M. No. 11897) consists only of the four fragments of an incomplete tooth cemented together. Its proportions and some of its other characters have been altered. Y.P.M. No. 10632, however, is a homologous tooth of this genus and all its characters may be checked on several other excellent specimens. The cusp formula is 7:8:6, but the posteroexternal, posterointernal and anteromedian cusps are smaller than the others. The outer and median rows are of about equal length and width. In the inner row the third to fifth cusps from the anterior end are the largest, and the row narrows anteriorly and does not extend as far forward as the other two. The cusps are crescentic in general form, the limbs of the crescents pointing forward.

In orienting these teeth Osborn naturally assumed the shorter, tapering cusp row to be external (1893, Pl. VII, fig. 8, also in *Cimolomys* [*Ptilodus*] fig. 4), but this is surely incorrect. In those multituberculates (save the Tritylodontidae) in which there are three upper molar cusp rows, the incomplete or tapering row is always internal, its widest end posterior, on  $M^1$  and external, its widest end anterior, on  $M^2$ . Osborn's left  $M^1$  is from the right side and *vice versa*.

$M^2$  of this genus was named *Tripriodon coelatus* by Marsh. The type, Y.P.M. No. 11853, is 6.6 mm. long and 6.4 mm. wide, being much more nearly equidimensional than in the specimens from South Dakota and Montana. The cusp formula is 3:3:4. The cusps of the median row are crescentic, although, as in  $M^1$ , modified by basal grooving. The cusps of both lateral rows are rounded on the side away from the midline but each sends a sharp crest toward the latter, curving also somewhat forward. The outer cusp row narrows posteriorly and is shorter than the other two.

Other teeth homologous with this differ in being somewhat larger, with small cuspules at the anterior ends of inner and outer rows and several minute cuspules continuing the outer row posteriorly. There may also be four distinct median cusps.

### *Cimolomys* Marsh 1889

1889. *Cimolomys*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 84.

DEFINITION.—Lower incisor slender, not strongly compressed, enamel smooth.  $P_3$



present,  $P_4$  relatively long and low with not less than eleven serrations. Molar cusps crescentic, but with complex basal grooves and ridges.  $M_2$  longer than broad, with six or more cusps. Posterior upper premolars elongate, with a main shearing series of seven or eight cusps and a basal anteroexternal series of three or four. Jaw relatively long and slender. Species smaller than those of *Meniscoëssus*.

TYPE.—*Cimolomys gracilis* Marsh.

DISTRIBUTION.—Lance formation, Wyoming; Hell Creek beds, Montana; Belly River formation, Alberta.

As here used, this genus probably includes two or three genera, possibly even more. By Osborn all of these Cretaceous smaller multituberculates were referred to the Paleocene (Torrejon, Fort Union) genus *Ptilodus*. That *Ptilodus* should occur in the Cretaceous is very improbable, *a priori*, and now proves to be demonstrably incorrect. The differences between multituberculate genera are always more clearly seen in the last upper premolar than in any other single tooth. In *Ptilodus* this tooth has two complete elongate longitudinal rows of cusps of about equal development and the rudiments of a third row at the anteroexternal edge of the tooth. From the Lance a number of homologous teeth are known which must be adequately representative of *Cimolomys*, even in its broadest sense and these always have only one complete row of cusps with the rudiments (or vestiges) of a second row anteroexternally. The two genera cannot be considered synonymous. The lower jaws, to be sure, are very similar, but the lower jaw pattern in the whole family is rather stereotyped. Species can be distinguished from lower jaws alone, but in many cases the generic characters are here rather obscure.

#### INCLUDED GENERA

1889. *Cimolodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 84. Type: *C. nitidus* Marsh.  
 1889. *Nanomys*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 85. Type: *N. minutus* Marsh. Non *Nannomys* Peters 1876.  
 1892. *Nanomyops*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 261. New name for *Nanomys*.  
 1889. *Allacodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 178. Type: *A. lentus* Marsh. Some of the material referred to this genus probably should be included in *Meniscoëssus* but the genoholotype probably belongs with the genera here included under *Cimolomys*.

#### *Cimolomys gracilis* Marsh 1889

1889. *C. gracilis*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 84.

TYPE.—Y.P.M. No. 11835. Isolated  $M^1$ .

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

DIAGNOSIS.— $M^1$  type 4.8 mm. long and 2.7 mm. wide. Cusp formula 6:8:9. Inner row as long as outer. Species used in a very broad sense for all of the smaller multituberculates from the Niobrara County, Wyoming, Lance beds.

## INCLUDED SPECIES

1889. *Cimolomys bellus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 84. Type: Y.P.M. No. 11778, isolated M<sup>2</sup>. Not figured.
1889. *Cimolodon nitidus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 84. Type: Y.P.M. No. 11776, isolated M<sub>1</sub>. Fig'd, Marsh 1889A, Pl. II, figs. 5-8.
1889. *Cimolomys digona*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 177. Type: Y.P.M. No. 11779, isolated M<sub>1</sub>. Fig'd, Marsh 1889B, Pl. VII, figs. 1-4.
1892. *Cimolodon parvus*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 254. Type: Y.P.M. No. 11777, symphysis of lower jaw with incisor. Fig'd, Marsh 1892A, Pl. VI, fig. 4.
1892. *Cimolodon agilis*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 255. Type: U.S.N.M. No. 2132, fragment of lower jaw with M<sub>1</sub>. Fig'd, Marsh 1892A, Pl. VI, fig. 8.
1889. *Nanomys minutus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 85. Type: Y.P.M. No. 11855, isolated M<sub>2</sub>. Fig'd, Marsh 1889A, Pl. II, figs. 9-12.
1889. *Halodon serratus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 87. Type: Y.P.M. No. 11811, isolated P<sub>4</sub>. Fig'd, Marsh 1889A, Pl. III, figs. 14-17.
1889. *Halodon formosus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 179. Type: Y.P.M. No. 11812, isolated P<sub>4</sub>. Fig'd, Marsh 1889B, Pl. VIII, figs. 36-39.
1889. *Allacodon lentus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 178. Type: Y.P.M. No. 11758, upper premolar. Fig'd, Marsh 1889B, Pl. VIII, figs. 22-26. Doubtfully included.
1889. *Allacodon pumilus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 179. Type: Y.P.M. No. 10372, upper premolar. Not figured. Doubtfully included.
1892. *Allacodon fortis*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 255. Type: U.S.N.M. No. 2137, upper premolar. Fig'd, Marsh 1892A, Pl. VII, fig. 4. Doubtfully included.
1892. *Allacodon rarus*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 256. Type: U.S.N.M. No. 2144, upper premolar. Fig'd, Marsh 1892A, Pl. VII, fig. 5. Doubtfully included.

The originals of the following figures are thus included in this broad species:

- Marsh 1889A, Pl. II, figs. 1-12.  
                   Pl. III, figs. 14-17.  
       1889B, Pl. VII, figs. 1-4, 13-16.  
                   Pl. VIII, figs. 17-39.  
       1892A, Pl. V, fig. 1.  
                   Pl. VI, figs. 1-2, 4, 6-9.  
                   Pl. VII, figs. 3-5.

These specimens certainly include several quite distinct species and possibly two or more closely related genera. If the discovery of good associated material ever permits a real revision, it will be possible to use many of Marsh's names. At present, however, direct comparison is impossible in so many cases that the validity or invalidity of the various names cannot be determined and they cannot be given separate definitions. Since all these forms are apparently closely related, *Cimolomys gracilis*, *sensu lato*, does name a morphological and taxonomic unit, although this unit is much larger than a species in the modern sense of the word.

## DENTITION

**LOWER INCISORS.**—There is a distinctive type of lower incisor which, as Osborn has pointed out, must from its invariably small size belong to the group here united under *Cimolomys*. Marsh also recognized the true affinities of these teeth and made one (Y.P.M. No. 11777) the type of his species *Cimolodon parvus*. It is slender, pointed, the median side concave, the outer convex. The tip is completely enameled. All of the extra-alveolar part of the tooth is covered with at least a light coat of enamel except for the posterosuperior part, toward the inner face. The enamel extends a short distance into the alveolus along the lower side. It is impossible to affirm positively that the larger forms did not have incisors more like those of *Meniscoëssus*, but in general the two seem very distinct, with no intermediates. There are, however, a number of possible variants and doubtful teeth and no multituberculate tooth is so easily confused with that of a reptile or of some other mammals.

**LOWER PREMOLARS.**—Y.P.M. No. 13692 has  $P_4$ ,  $M_1$ , and  $M_2$  in association and hence puts the characters of the lower cheek teeth in the genus beyond much question. The premolar is badly worn, but permits close comparison with perfect isolated specimens. The following comparisons are instructive:

Species	$\frac{\text{Length } P_4}{\text{Length } M_1}$	$\frac{\text{Length } P_{1-4}}{\text{Length } M_1}$
<i>Ctenacodon serratus</i>	1.31	3.00
<i>Meniscoëssus</i> sp.	0.92	...
<i>Cimolomys</i> sp.	1.60	...
<i>Ptilodus mediaevus</i>	2.30	...

*Ctenacodon* probably represents approximately the structurally ancestral condition. *Ptilodus* has about the same relative shearing power, but it is concentrated in a single tooth rather than three ( $P_{2-3}$ ,  $P_1$  being hardly shearing in *Ctenacodon*). *Cimolomys* has a relatively much shorter shearing blade than *Ptilodus*, although it was still very important and although the opposing upper tooth was even more perfectly adapted for this purpose. *Meniscoëssus* shows the greatest reduction in relative length of the blade although, as has been shown, it is here still well developed and shows no loss of function.

The size of  $P_4$  varies about as much as does that of the molars (below), but its proportions remain about the same. The number of serrations varies from eleven in the smaller to fourteen in the larger specimens.

$P_3$  has eluded the collectors, but its alveolus is known and it was obviously like that of *Meniscoëssus* or *Ptilodus*.

**LOWER MOLARS.**—The type of *Cimolodon nitidus* (Y.P.M. No. 11776) is a first lower molar. It measures 4.5 mm. in length by 2.0 mm. in width and has a cusp formula of 8:4. The outer cusps, of which the first two are small, are crescentic but less strongly so than in *Dipriodon*. The tips appear as if they had been bent forcibly backward over the anterior slopes of the succeeding cusps. The inner cusps are larger, point somewhat backward, and are faintly crescentic, although this is somewhat obscured by



the two or three strong ridges which run outward on the slope of each cusp toward the midgroove. Another type of  $M_1$  is seen in Y.P.M. No. 13681, with the formula 6:4 and measuring 2.3 mm. by 1.0 mm. The cusps resemble those of the tooth just described save that they are more distinctly crescentic. The following data from a few of the unbroken teeth in the Yale collection will give some conception of the variation and show clearly that several species are present:

Y.P.M. No.	Length	Cusp Formula
13686	2.0	6:4
13688	2.1	6:4
13681	2.3	6:4
10618	2.8	7:5
13687B	3.2	7:5
13684B	3.7	8:4
13683	3.9	8:5
13689	4.0	6:4
13687A	4.1	7:5
13684A	4.3	7:5
11776	4.5	8:4
13682	4.5	7:5

$M_2$  is exemplified by the type of *Nanomys minutus* Marsh, Y.P.M. No. 11855. It measures 3.0 mm. in length and 2.2 mm. in width. Its cusp formula is best expressed as 4:2, although the posterior two cusps of the outer row are in contact almost to their tips and posterior to the last one a ridge runs around the posterior end of the tooth which probably bore several small cuspules when unworn. The two inner cusps are massive, but they occupy only about two-thirds as much space as does the outer row. The anterior border is squarely transverse, the posterior strongly oblique. Another tooth, almost identical in character but unworn, shows the ridge around the posterior end of the midgroove to have borne seven or eight minute tubercles. The central groove has the usual pattern of irregular, sharp, narrow, anastomosing ridges.

Quite a different type of  $M_2$  is seen in Y.P.M. No. 10399b. The cusp formula is 7:2. The outer cusps have their bases confluent, only the tips rising free, and from each tip a strong ridge runs downward and backward into the midgroove. The posterior of the two stout inner cusps sends five similar ridges into the midgroove. The other variants are less distinctive. The size range is rather less than for some other parts of the dentition, probably because the smallest forms would be very difficult to find.

UPPER INCISORS.—The upper incisors of this group are not surely known. The large incisors with bifid tip were apparently confined to *Meniscoëssus*, or at least no teeth of this character in the collections appear to be small enough for *Cimolomys*. Marsh assigned to this genus some teeth with three accessory cusps of decreasing size posterior to the main point. The possibility that these are multituberculate incisors is not flatly denied, but they are quite unlike those of any other member of the order. They may be reptilian. Osborn (1893) states, "The median upper incisors are short crowned and slightly notched at the back; they are closely applied with oblique pos-

terior faces, in which the dentine is exposed. . . .” Teeth of this sort are not uncommon, but they may be I<sup>8</sup> of *Meniscoëssus*. Some forms of *Cimolomys* may have resembled *Ptilodus* in having such simple upper incisors that they could hardly be recognized as such in individual specimens.

UPPER PREMOLARS.—The last upper premolar of this group is readily identified and was correctly associated by both Marsh and Osborn. Y.P.M. No. 10375 (Marsh 1892A, Pl. VI, fig. 2) is typical. It belongs with one of the smaller forms, measuring only 3.0 mm. by 1.4 mm. The main feature is a long sharp crest which bears seven cuspules, the sixth the largest. Posterointernally the tooth slopes out into a small heel which may have borne a cusp now removed by wear. External to the first four cusps of the shearing crest is a parallel series of four cusps. These are low on the crown, almost basal in character, but individually they are larger than those of the main crest. In another small type (Y.P.M. No. 13718), 4.9 mm. in length, the posterointernal heel is less developed, there are only three cusps in the anteroexternal accessory row, and posterior to the main crest is a pair of small basal cuspules opposite each other transversely. Twenty-five or thirty teeth of this general type have been examined. They show about the same range of size as do the other teeth included in this group.

The anterior upper teeth of this group are seen in Marsh's *Allacodon*. *A. lentus* has five conical cusps arranged in two transverse pairs and with the fifth at one end of the tooth in a median position. *A. pumilis* has four cusps arranged in a square, one pair stouter than the other, and *A. rarus* is of essentially the same type. *A. fortis* has three subequal cusps in a triangle. Now that the upper dentition of *Ptilodus* is well known, it is clear that these different types owe their characters more to position in the series than to systematic differences. In *Ctenacodon* there are three tricuspid premolars followed by two multicuspid shearing teeth. In *Ptilodus* there are in series a tricuspid tooth, a quadricuspid one, and a quadri- to sexcuspid one, followed by a single multicuspid shearing tooth. In U.S.N.M. No. 2138 (incorrectly said to be the type of *A. pumilis* in the Catalogue of types, etc., in the National Museum) the three anterior upper premolars of a member of this group are preserved in actual association (Marsh 1892A, Pl. VII, fig. 3). The first two teeth are tricuspid, the third quadricuspid. These were probably followed by the shearing tooth, although it is possible that another tooth with four to six cusps intervened. The latter would be contrary to analogy with *Ptilodus*, however, and it is more likely that the teeth in the collections with five and six cusps belonged to different species and occupied the position of the quadricuspid tooth in this series.

UPPER MOLARS.—*Cimolomys* was originally based on a first upper molar, Y.P.M. No. 11835. It measures 4.8 mm. by 2.7 mm. and has a cusp formula of 6:8:9. The inner row is slightly narrower anteriorly, but it is as long as the other two rows, a very unusual character among Ptilodontidae. *Cimolomys bellus* was also based on a first upper molar, Y.P.M. No. 11778. It is 3.0 mm. long and 1.6 wide and has a formula of 6:7:7. The last cusp of the outer row is small and all those of the inner row are small. The inner row narrows anteriorly and quite disappears opposite the posterior end of the second cusp of the median row. *C. digona*, Y.P.M. No. 11779 is larger, measuring

6.0 mm. by 2.8 mm. and has a remarkably high cusp number, 9:10:8. The posterior cusps of the outer and median rows are small as are the anterior ones of the median row. In all the collections many variations are seen, mostly in rather minor details, which it would serve no useful purpose to describe at length. The following figures give some idea of the range:

Y.P.M. No.	Length	Cusp Formula
10399A	2.1	6:7:4
13709	2.4	6:7:5
13714	2.4	6:8:5
13712	2.7	7:8:6
11778	3.0	6:7:7
13715	3.0	6:8:5
13713	3.1	7:9:5
10399B	3.6	6:8:6
13707	3.8	6:8:5
10399D	4.3	6:7:6
10457A	4.3	6:8:8
10457B	4.4	6:7:8
13708	4.4	6:7:8
13710	4.4	6:7:6
13705	4.5	7:8:8
11835	4.8	6:8:9
13706	4.9	6:8:6
13711	5.1	7:8:9
11779	6.0	9:10:8

From the grouping of these and other figures and from the morphological variations one has the impression of from three to six species belonging to at most two or three very closely related genera.

The type of *Selenacodon brevis*, Y.P.M. No. 11876, is the last upper molar of a large member of this group. It measures 3.3 mm. in length and 3.0 in width. The cusp formula is 6:4:3 and the cusps are shaped as in the preceding tooth, or much as in Ptilodontids generally. The first five cusps of the outer row are subequal, the last very small. In the middle row there are only three truly crescentic cusps, the anterior one being developed as a transverse ridge which runs over to the inside border anterior to the inner row. The three cusps of the inner row decrease in size from front to back and the last is opposite the third cusp of the median row. Comparable teeth are numerous, about twenty specimens having been studied carefully. They show the usual range of variation. The transverse ridge anterior to the middle and inner rows is soon cut through so that in older individuals it may appear to add a cusp to the inner row. In one type, Y.P.M. No. 13717, this ridge is enlarged into a true anterior cusp in the inner row, the formula being 5:4:5. A smaller type is seen in Y.P.M. No. 13716 with a formula of 4:3:2, or perhaps 4:3:3 when unworn, with the transverse anterior ridge confined, even before wear, to the middle row. Other minor variants occur.



*Cimolomys primaevus* (Lambe 1902)

1902. *Ptilodus primaevus*, Lambe, *Contrib. Canad. Pal.*, XXX, 79.

TYPE.—Geol. Surv. Canada. Right lower jaw with  $P_4$  and  $M_1$ . Fig'd, Lambe 1902, Pl. XV, figs. 13-14.

HORIZON AND LOCALITY.—Belly River beds, Alberta, Canada.

DIAGNOSIS.— $P_4$  with eleven serrations.  $M_1$  formula 6:4. Specific or generic characters inadequately known.

This specimen is important as the only known multituberculate from this horizon. The original has not been studied by the present writer, but Lambe's description and figures are clear. The dental characters are given as follows: "Fourth premolar with eleven serrations on its edge; on its inner side, five complete grooves preceded by a half groove. First molar with four tubercles on its inner side and six tubercles on its outer side. . . . There is a slightly backward curve of the tubercles on the outer side of the first molar. . . ." Matthew (1916) stated that Lambe's type is "certainly related to *Cimolomys* of the Lance and apparently not generically separable." From what is now known, even the species cannot be proven to be distinct from that of some of the Lance specimens. It is so improbable that a species, or even a genus, of mammals is really common to these two very distinct faunas, however, that further material would almost surely serve to separate *C. primaevus* from any Lance form.

*Essonodon* Simpson 1927

1927. *Essonodon*, Simpson, *Amer. Mus. Novitates*, No. 267, 2.

DEFINITION.— $M_2$  broader than long, cusp formula 3:2, two external roots, and one internal.

TYPE.—*E. browni* Simpson.

DISTRIBUTION.—Hell Creek beds, Montana.

This genus is very poorly known but it is quite noteworthy from a morphological point of view in the extreme anteroposterior compression of  $M_2$  and its small cusp number.

*Essonodon browni* Simpson 1927

1927. *E. browni*, Simpson, *Amer. Mus. Novitates*, No. 267, 2.

TYPE.—Amer. Mus. No. 14410. Isolated  $M_2$ . Fig'd, Simpson 1927, fig. 1.

HORIZON AND LOCALITY.—Hell Creek beds, Crooked Creek, Montana.

DIAGNOSIS.—Sole known species of the genus.  $M_2$  2.4 mm. long, 3.6 mm. wide.

## ORDER MARSUPIALIA Illiger 1811

DEFINITION.—Primitive cheek tooth formula  $P_3^3 M_4^4$ . Typically with replacement confined to last premolar. Angular process of lower jaw inflected (save in *Tarsipes*). Typically with nasals expanded posteriorly, jugal taking part in glenoid fossa, and

occipital exposure of mastoid large. Palatal vacuities usually present. Optic foramen confluent with sphenorbital fissure. Internal carotid piercing basisphenoid (save in *Acrobates*). Epipubic bones generally present.

DISTRIBUTION.—Cretaceous, North and South America. Paleocene, Europe and North America. Eocene and Oligocene, Europe and North and South America. Miocene, Europe and South America. Pliocene, South America and Australia. Pleistocene and Recent, North and South America and Australia. This known distribution is obviously fragmentary. They were probably continuously present in North and South America and in Australia from the Cretaceous to recent time and in Europe from the Cretaceous to the end of the Miocene.

Various of the forms here gathered together under the Marsupialia have been referred to all three of the major recent groups of mammals and also to the Jurassic Trituberculata (Pantotheria). Marsh (especially 1892B) recognized the fact that most of them are marsupials and placed them in a family Cimolestidae, but he believed that insectivores and pantotheres were also present. Osborn (1893) at first considered *Thlaeodon* as a possible monotreme and suspended judgment as regards the other genera. Later, however, he considered certain genera now believed to be didelphid as "capable of giving origin to the teeth of the Amblypoda." (Osborn 1898, p. 172.) In the latest study of the problem, Matthew (1916, p. 481) states: "While for various reasons it seemed probable that most or all of these Cretaceous trituberculates were marsupials, there was no conclusive proof of it. On the other hand there was not and is not any valid evidence for placing any of them in the placental group," and he goes on to prove that the only two genera which he considers as really determinable are certainly marsupial.

The necessarily confused taxonomic status of these fragmentary remains, so strongly stressed by Matthew, is unfortunate, but does not alter the fact that reasonably certain conclusions as to the diversity and the broader phylogenetic and adaptational features of the fauna are possible. The present writer believes, with Matthew, that the majority of the "trituberculates" are demonstrably marsupials, but insists that placentals are also present, *Gypsonictops* certainly and *Batodon* and *Telacodon* probably belonging to the higher subclass.

Osborn's method of approaching the revision of the Cretaceous marsupials still seems the most practical. He emphasized (1893) the importance of basing taxonomic results chiefly on the upper molars, so far as possible, and of not attempting to refer teeth from other parts of the dentition not actually found in association. In the present memoir the taxonomy is based chiefly on upper molars save where names have already been given by Marsh to lower molars. Warrantable exceptions are to be made only of the few relatively complete lower jaws (e.g., *Eodelphis cutleri*) which really do provide an adequate taxonomic basis. Teeth are referred to a definite genus only when directly comparable with the genoholotype. As with the multituberculates, the genera are used in a very broad sense, in some cases certainly including two or more related genera, and no attempt is usually made to distinguish species beyond the type species of genera.



## DIDELPHIIDAE Gray 1821

DEFINITION.—Dental formula  $I_{4-3}^{5-2} C_1^1 P_3^3 M_4^4$ . Incisors small. Canines large. Premolars simple, trenchant or bulbous. Lower molars tuberculo-sectorial, with three trigonid cusps and basined heels with hypoconulid posteriointernal, near entoconid. Upper molars tritubercular, trigonal, with no true hypocone. External cingulum broad, shelf-like, with various well-defined external marginal cusps. Quadrupedal, plantigrade, usually with opposable hallux and pollex, often with prehensile tail.

TYPE.—*Didelphis* Linnaeus.

DISTRIBUTION.—Known: Cretaceous, North and South America. Paleocene, Europe and North America. Eocene and Oligocene, North and South America and Europe. Miocene, South America and Europe. Pliocene, South America. Pleistocene and Recent, North and South America. Inferred: Probably world-wide (save perhaps in Africa) in Cretaceous. In America surviving to the present time. In Europe becoming extinct at the end of the Miocene. In Asia becoming extinct at some unknown time. In Australia becoming modified in the early Tertiary into the families typical of this continent.

The Cretaceous marsupials were apparently all intended by Marsh to be referred to his family Cimolestidae. This family has not been defined and the type genus was based on a lower molar. It would be possible to define the family on the basis of referred upper teeth, but it is poorly known and it certainly differed very little from the Didelphiidae. For this reason the family Didelphiidae is used in a broad sense and is made to include all the primitive opossum-like fossils of North and South America and Europe, not only the Cimolestidae but also the Microbiotheridae of Ameghino. In so far as they are clearly recognizable as distinct groups, the more distinctive of the fossil forms may be placed in separate subfamilies, the number and arrangement of which will naturally be altered by further discoveries. At present four subfamilies are clearly distinguishable:

1. *Pediomyinae*. Premolars trenchant. Upper molars didelphine in contour. Paracone and metacone subequal. Cingulum on  $M^{1-3}$  narrow anteriorly, oblique, prolonged posteriorly into a sharp metastylar spur. Paraconule definite, connected by a slight crest with the anterior style. Second style absent or weak, fourth larger than third (median).

2. *Didelphodontinae*. Premolars bulbous, crushing. External cingulum of upper molars uniformly broad, bilobed, nearly symmetrical, without marked metastylar or parastylar spur. Paracone and metacone subequal. Second style large and heavy, others variable.

3. *Microbiotheriinae*. Premolars trenchant. On  $M^{1-3}$  metacone somewhat larger than paracone. No distinct metastylar spur. External cingulum moderately developed, of about equal width throughout, styles not strong.

4. *Didelphiinae*. Premolars trenchant. On  $M^{1-3}$  paracone much reduced. Cingulum strong, produced into a marked metastylar spur. Second style large, fourth smaller than third. Paraconule reduced or absent, not connected with anterior style.



The Pediomysinae include the more primitive Cretaceous forms and probably some or all of the Paleocene ones. This is the most primitive subfamily and apparently represents the structural ancestry of the whole family, or indeed of the whole order. The Didelphodontinae are known only from the North American upper Cretaceous and represent an aberrant group of durophagous adaptation. The Microbiotheriinae are confined to the Tertiary of South America. Although often given a very central position, as by Ameghino, they are probably somewhat aberrant and are probably not directly ancestral to any living didelphines, which they seem to resemble rather less than do some of the Pediomysinae. The subfamily Didelphiinae includes all of the living opossums and the Tertiary forms except the microbiotheriines. It is, on the whole, more primitive than either Microbiotheriinae or Didelphodontinae and possibly is directly descended, with some modification, from the Pediomysinae.

In the Cretaceous the Pediomysinae and Didelphodontinae are represented, but at present it is impossible to assign all of the named genera to one or the other family. The following are surely members of the Pediomysinae: *Pediomys*, *Nyssodon*. The following surely belong in the Didelphodontinae: *Didelphodon*, *Ectoconodon*, *Thlaeodon*, *Alphadon*, *Stagodon*. *Eodelphis* and *Euangelistes* include only lower teeth as yet, but are probably pediomyine, and *Diaphorodon* is closely similar to *Eodelphis*. *Cimolestes*, *Delphodon*, and the unnamed types of lower teeth are of doubtful affinities.

## A. GENERA INCLUDING UPPER MOLARS

### *Pediomys* Marsh 1889

1889. *Pediomys*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 89.

DEFINITION.—Upper molars pediomyine, molar cusps relatively low. Pa and me well separated. No prominent cingula on base of pr.

TYPE.—*P. elegans* Marsh.

DISTRIBUTION.—Lance, Wyoming. Hell Creek, Montana.

### INCLUDED GENUS

1898. *Protolambda*, Osborn, *Bul. Amer. Mus. Nat. Hist.*, X, 172. Type: *P. hatcheri* Osborn.

This genus, *sensu lato*, is a very large one, including the greater number of Lance didelphids. Two or more genera may be included, although if so they are very closely related. Certainly there are a number of species, but none can be usefully defined at present. *Protolambda* Osborn is based on a tooth larger than the type of *Pediomys elegans* and his specimen may be retained as specifically distinct, although it shows no distinctions of true generic character. The original diagnosis and figure did not separate *Protolambda* from *Pediomys* except for the fact that the types of the former are labeled as if from the left side, although all three are really right upper molars.

Of the older figures, the following are of specimens now referred to *Pedionmys*:

Marsh 1889A, Pl. IV, figs. 23-25.

1892A, Pl. IX, fig. 1.

Pl. X, fig. 3.

Osborn 1893, Pl. VIII, A, B.

1898, fig. 1, A.

*Pedionmys elegans* Marsh 1889

1889. *P. elegans*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 89.

TYPE.—Y.P.M. No. 11866. Isolated upper molar, broken and weathered. Fig'd, Marsh 1889A, Pl. IV, figs. 23-25.

NEOTYPE.—Carnegie Mus. No. 11658. Upper jaw with M<sup>2-4</sup>. Fig'd, Simpson 1929B, fig. 3.

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming. Referred specimens from Dawson County, Montana.

DIAGNOSIS.—Not precisely definable. Used in a broad sense for the smaller forms of *Pedionmys* from the Lance and its equivalents.

Several species are clearly represented in the material referred to *P. elegans*. The known characters of the genus as a whole are given below, under *P. hatcheri*.

*Pedionmys hatcheri* (Osborn 1898)

1898. *Protolambda hatcheri*, Osborn, *Bul. Amer. Mus. Nat. Hist.*, X, 172.

SYNTYPES.—Amer. Mus. Nos. 2201, 2202, 2203.<sup>29</sup> Isolated right upper molars. Fig'd, Osborn 1898, fig. 1, A.

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

DIAGNOSIS.—Not exactly definable. Used in a broad sense for the larger forms of *Pedionmys* from the Lance and its equivalents.

Under this head all of the teeth definitely referable to the genus may be described.

DENTITION

The genoholotype, Y.P.M. No. 11866, is very badly preserved, although sufficiently clear to validate the genus. Y.P.M. No. 10682 (Fig'd, Marsh 1892A, Pl. X, fig. 3) is closely similar and better preserved. It is apparently a second or third upper molar of the right side. The crown consists essentially of a nearly symmetrical trigon. The protocone is stout, relatively blunt, subcrescentic, without anterior or posterior basal cingula. On the external slope of the pr are the two conules, which are small, crescentic, and of about equal size. The anterior ridge of the paraconule continues externally at the level of the crown and rises into the anterior stylar cusp, A (below), while the corresponding posterior crest of the metaconule runs outward and upward toward the base of the tooth and then disappears. The median ridges of the two conules

<sup>29</sup> Osborn states that the types are four molars, but he only designates and figures these three.

do not meet each other, but run to the bases of their respective primary cusps, the paracone and metacone. The latter are higher than the protocone and more slender. They have sharp anterior and posterior ridges, but are only slightly compressed transversely. The external cingulum is very well developed. From a study of very numerous Cretaceous didelphid upper molars as well as of a large series of later didelphids from all known horizons, it is apparent that the ancestral didelphid had typically five styler cusps, the history of each of which may usually be followed with some clarity. Bensley's notation for the didelphid styles, being based on much later forms only, is not readily applicable and the writer proposes a modification of it, designating the five primary styles A, B, C, D, and E respectively, from anterior to posterior. (See Fig. 43.) In the present tooth A is anterior and very slightly external to the paracone, while C and D are small and ridge-like.

The following are the most striking variations seen in teeth of this general type:

1. The width varies from about 2.5 mm. to about 6.0 mm.
2. The proportions vary. Some are about as broad as long, others much broader than long. This is largely due to position in the dental series,  $M^4$  being much more transverse than  $M^1$ .
3. Some molars are much more oblique than others—also due largely to position.
4. The external border may be a straight oblique line or it may run almost anteroposterior opposite the pa and then turn rather abruptly outward. The cingulum may be obsolete opposite the pa. The latter is due, at least in part, to position in the series also, as the cingulum opposite the pa is less developed on  $M^{1-2}$  than on  $M^{3-4}$ .
5. The styler cusps vary considerably. A is always present and is only slightly external to the pa save on  $M^4$ . B is never well developed, while C and D are about equally developed and usually form ridge-like crests parallel to the outer border. In some cases, however, they are cone-like and this marked difference is probably of systematic value. E is always present save on  $M^4$ .

On teeth supposed to be first molars, the pa and me are approximated to the pr, crowding the conules, B is practically absent, C is represented, if at all, only by small median tubercles, and E is slightly coarser than usual.

Last molars, such as Y.P.M. No. 13650, differ radically from the above, but in just the same way as  $M^4$  of *Didelphis* differs from the preceding teeth.  $M^4$  is strongly

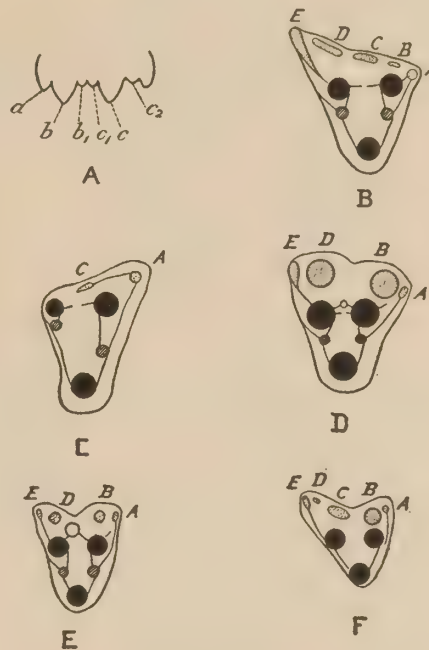


FIG. 43. Didelphid upper molars. A, Bensley's styler designations. B, *Pedionomys*, showing five primitive styler cusps and their suggested designations. C, last upper molar of *Pedionomys*. D, *Ectoconodon*. E, *Alphadon*. F, *Didelphis*.



oblique, with a pronounced external spur, but in this case the spur is parastylar, not metastylar as in  $M^{1-3}$ . A forms the end of this spur. B is absent, C slightly developed. D and E are absent and the cingulum is obsolete posteriorly. The metacone is reduced and the metaconule approximated to it.

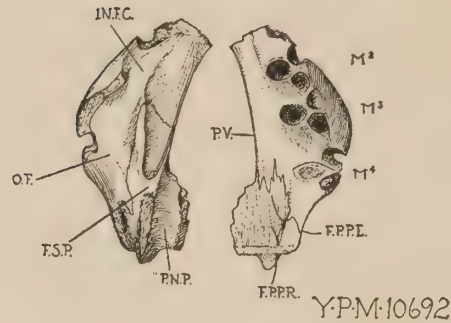


FIG. 44. *Pediomys* sp. Left half of palate. Superior and inferior views.  $1\frac{1}{2}$  times natural size.

F.P.P.E., bristle passing through posteroexternal palatine foramen. F.P.P.R., bristle passing through small foramen in postpalatal ridge. F.S.P., sphenopalatine foramen. IN.F.C., floor of infraorbital canal. O.F., floor of orbit. P.N.P., posterior narial passage. P.V., edge of palatal vacuity.

#### SKULL

Various small fragments of the skull of this genus are known, the most important being Y.P.M. No. 10692 (see Fig. 44), the posterior left portion of a palate without teeth. Its chief interest lies in its close agreement with the recent *Didelphis*. The structure is well shown in the accompanying figure and has no feature which may not be found in the recent opossum. This is the specimen to which Marsh had reference (1889B, p. 179) when he suggested that the rounded margins of the vacuity might indicate that it was functional as the posterior nares, but the vacuity is equally well rounded in many recent specimens, and it is inconceivable that it can ever have had this function.

#### *Nyssodon* Simpson 1927

1927. *Nyssodon*, Simpson, *Amer. Jour. Sci.* (5) XIV, 124.

DEFINITION.—Primary cusps of typical upper molar all slender and high, pa and me closely approximated, with connate bases. Narrow anterior and posterior cingula on base of pr. No median stylar cusps.

TYPE.—*N. punctidens* Simpson.

DISTRIBUTION.—Lance, Wyoming.

This genus is obviously quite distinct from anything that could be referred to *Pediomys*. There is a possibility that it is not a didelphid, but in view of the abundance of didelphids in the Lance and of a certain fundamental resemblance to *Pediomys* it may be considered as a pediomyine at least until it is better known.

#### *Nyssodon punctidens* Simpson 1927

1927. *N. punctidens*, Simpson, *Amer. Jour. Sci.* (5) XIV, 124.

TYPE.—Y.P.M. No. 13654. Isolated upper molar.

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming. The type is from Hatcher's Quarry 9 mammal locality, see Lull 1915A.

DIAGNOSIS.—Sole known species of the genus.

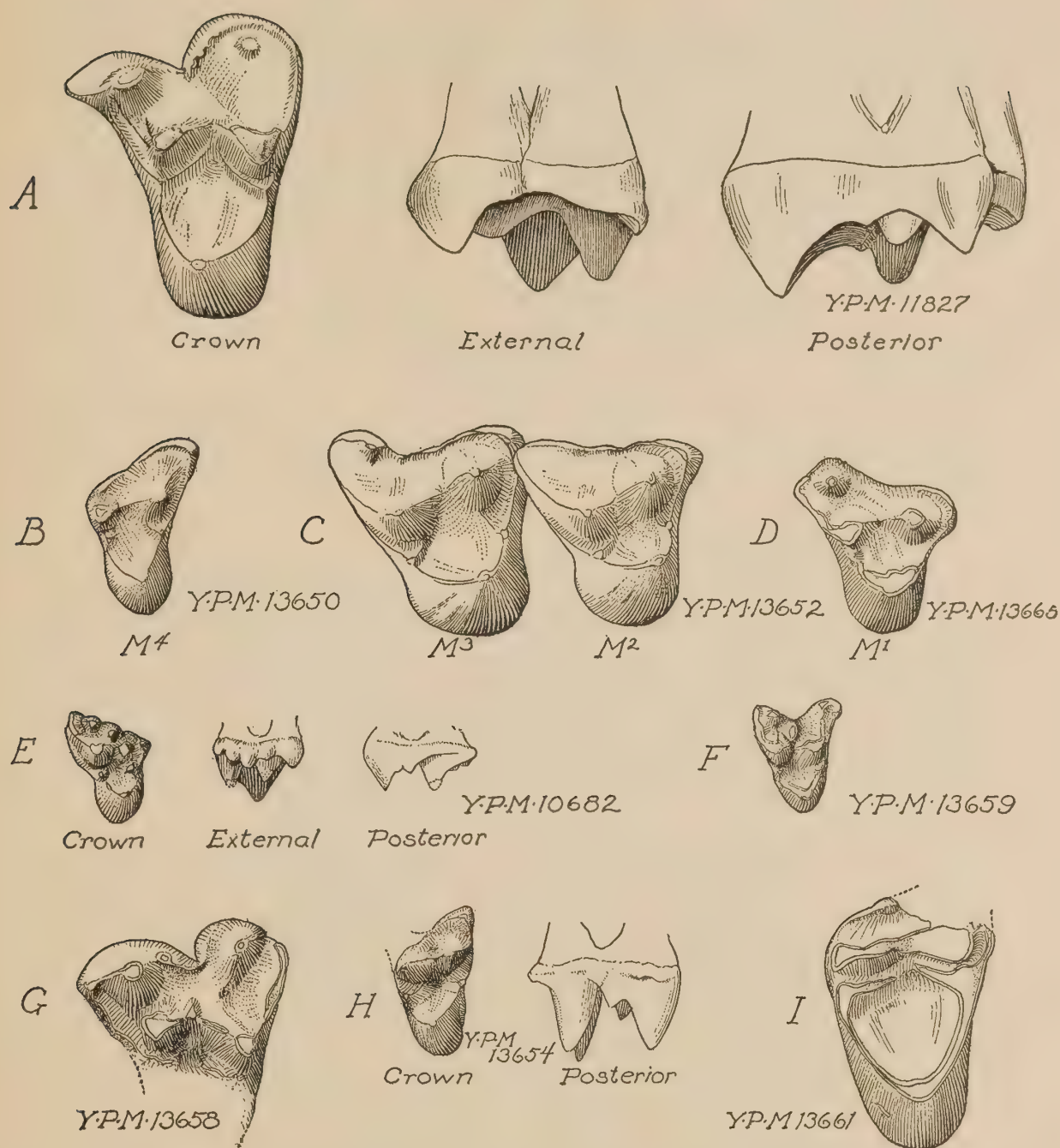


FIG. 45. Lance didelphid upper molars. A, *Didelphodon vorax*, type. B-D, *Pediomys* (or *Protolambda*) *hatcheri*, M<sup>4-1</sup>. E, *Pediomys* sp., F, *Alphadon marshi*, type. G, *Ectoconodon* sp. H, *Nyssodon punctidens*, type. I, Didelphodontine, last upper molar. All six times natural size.

The primary cusps are all very slender and high, the conules are well developed, and the pa and me are closely approximated, with a common base, and strongly compressed transversely. The pa is slightly higher than the me and the latter is of about the same height as the pr. The external cingulum is pediomysine in form, with a strong metastylar spur but without median stylar cusps. The presence of very narrow ledges on the anterior and posterior sides of the base of the protocone is noteworthy as indicating the first tendency to form cingula here. This piercing type of tooth is quite different in adaptational tendency from those of *Pedimys* and represents the opposite extreme from *Didelphodon* (below).

*Didelphodon* Marsh 1889

1889. *Didelphodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 88.

1889. *Didelphops*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 179.

DEFINITION.—Based on didelphodontine upper molars with stylar cusp B well developed, larger than the paracone. No median outer cusp. D small. E large and ridge-like.

TYPE.—*D. vorax* Marsh.

DISTRIBUTION.—Lance, Wyoming.

Besides the genotype, Marsh assigned two other species to this genus. *D. ferox* was based on a badly worn and broken lower molar. Reference to this genus does not rest on any direct evidence. *D. ferox* is synonymous with "*Cimolestes*" *curtus*, but the latter species does not belong in the genus *Cimolestes*. *D. comptus* was also based on an isolated lower molar. It is not congeneric with *D. ferox*. These lower teeth are treated below. For the present the name *Didelphodon* must be confined to upper molars directly comparable with the genoholotype. The two associated upper molars referred to *D. vorax* (Marsh 1892A, Pl. IX, fig. 1) belong to *Pedimys hatcheri*.

The name *Didelphodon* was changed to *Didelphops* by Marsh on the basis of essential preoccupation by *Didelphodus*. Such changes are sanctioned, or even demanded, by many writers and the matter may be one of personal opinion. Unfortunately the International Rules of Zoölogical Nomenclature deal with the matter only in a recommendation,<sup>80</sup> but this recommendation the writer prefers always to follow. Such action certainly makes for greater stability in zoölogic nomenclature as a whole, and can seldom lead to any real confusion. When two names of *closely related* animals differ only by one or two letters and cannot be considered as homonyms under Art. 35, special action may occasionally be necessary, but not by a single worker.

*Didelphodon vorax* Marsh 1889

1889. *Didelphodon vorax*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 88.

1892. *Didelphops vorax*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 262.

<sup>80</sup> Under Art. 36. ". . . When once introduced such names are not to be rejected on this account. Examples: . . . *Polyodus*, *Polyodon*, . . ."



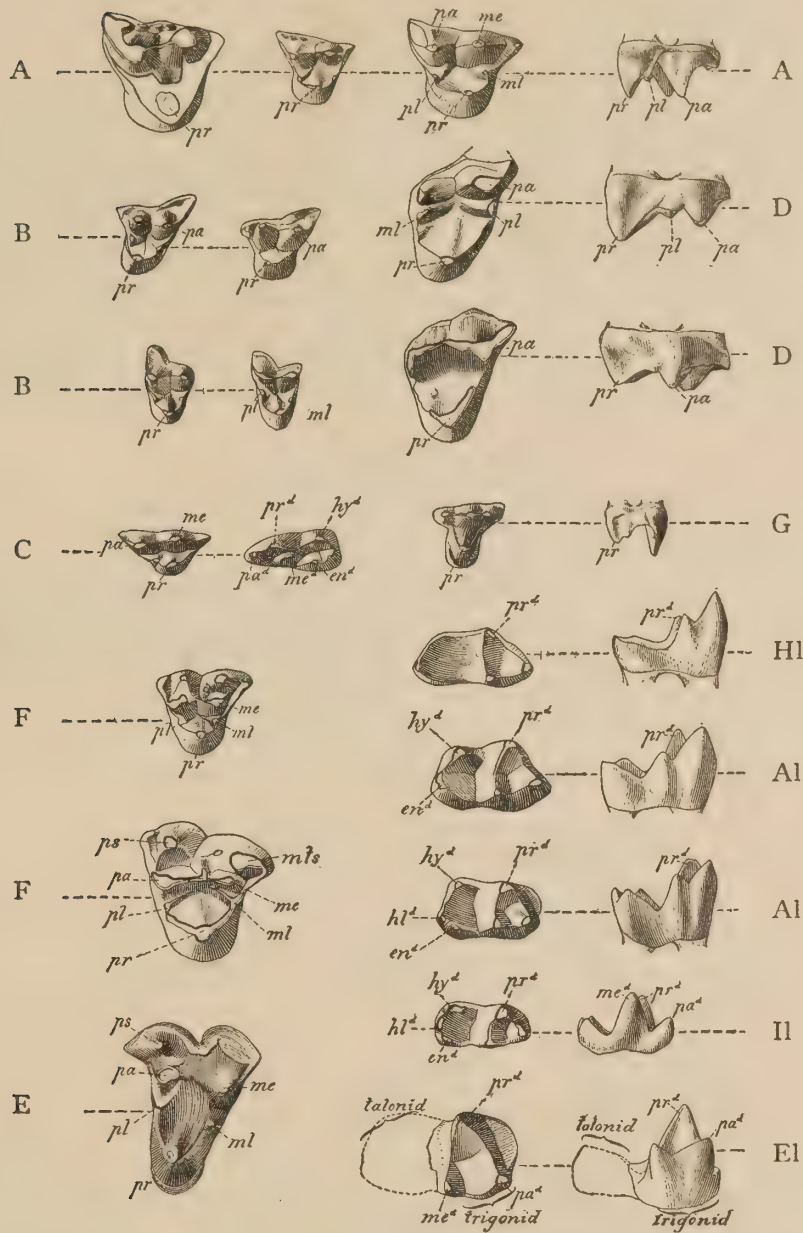


FIG. 46. Lance didelphids and ? insectivore. A-B, *Pediomys*, sensu lato. A, cotypes of *Protolambda hatcheri*. C, *Synconodon sexcuspsis*, cotypes. D, didelphodontine last upper molars. E, *Didelphodon vorax*, type. F, *Ectoconodon* (the lower figure is of the type of *E. petersoni*, and is a right molar, not a left as labeled). G, *Gypsonictops*? H1, A1, I1, E1, various lower molars. Reproduction of Osborn 1893A, Pl. VIII.

TYPE.—Y.P.M. No. 11827. Isolated upper molar. Fig'd, Marsh 1889A, Pl. IV, figs. 1-3.

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

DIAGNOSIS.—Sole known species referable to the genus as here defined.

The primary cusps are large and stout, but not high. The conules are small and near the pa and me. The cingulum is very broad and is divided into two nearly equal lobes by a deep median cleft. Both styles A and B are considerably external to a line through the pa and me. B is unusually large, being higher than the pa. There is no true median style, although the edge of the shelf is slightly nodulated between B and the locus of D. E is large and blunt and takes the form of a ridge running externally from the posterior slope of the me, while D is either absent or represented by a small tubercle on the anterior slope of E.

*Thlaeodon* Cope 1892

1892. *Thlaeodon*, Cope, *Am. Nat.*, XXVI, 759.

DEFINITION.— $P^8$  very heavy, wider than long, of blunt, crushing type.  $M^1$  apparently close to that of *Ectoconodon* (below), but D more conical and marginal and E a ridge not reaching the external margin, also whole tooth shorter and wider as well as much larger. Lower jaw short and heavy,  $P_3$  longer than wide, but blunt and heavy. Both  $P_2$  and  $P_3$  larger than any of the lower molars.

TYPE.—*T. padanicus* Cope.

DISTRIBUTION.—Lance, South Dakota.

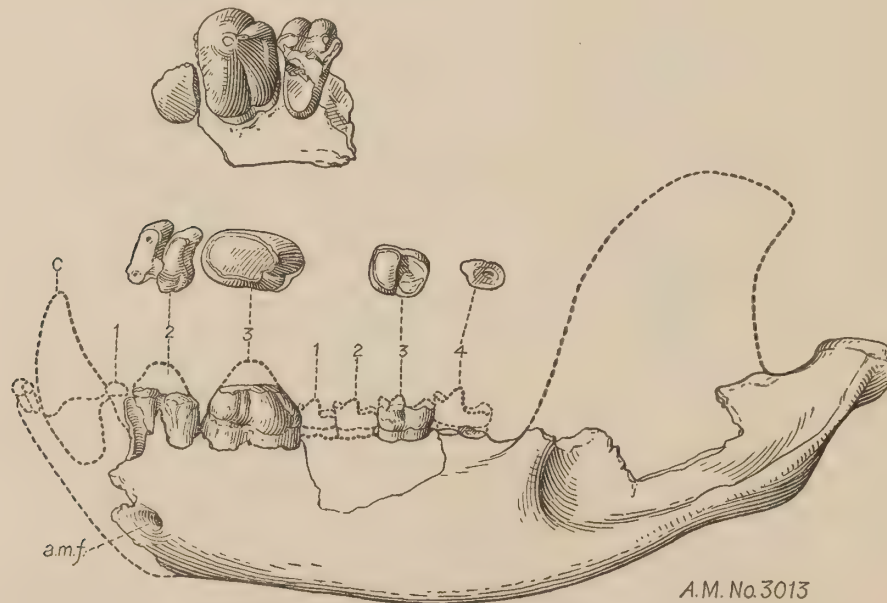


FIG. 47. *Thlaeodon padanicus*, upper jaw fragment, lower jaw and crown view of lower teeth, type specimen, No. 3013, three halves natural size: a.m.f., anterior mental foramen. (After Matthew, 1916.)

This is the only American Cretaceous genus in which associated upper and lower teeth are known, but it is none the less based on an annoyingly inadequate type. The single preserved upper molar,  $M^1$ , and single preserved lower molar,  $M_{2,3}$ , are both so badly worn and broken that direct comparison with the previously established Lance genera is difficult. It may belong to *Didelphodon*, as the upper molar resembles the type of the latter genus rather closely in size and proportions. The only striking difference is the apparent greater development of style D, and this may not be of generic value. In this one character it is more like *Ectoconodon*, but otherwise it differs more markedly from Osborn's (later) genus, as indicated in the definition. So far as one can judge from the lower molar, it might be the same as almost any of the largest Niobrara County Lance lower molars. Its recognition as a distinct genus is provisional and is justified chiefly by the importance given it by its relative completeness.

*Thlaeodon padanicus* Cope 1892

1892. *T. padanicus*, Cope, *Am. Nat.*, XVI, 759.

TYPE.—Amer. Mus. No. 3013. Part of left lower jaw with  $M_{2,3}$ ,  $P_3$ , and roots of  $P_2$ , and associated fragment of left maxilla with  $P^3$  and broken  $M^1$ . Fig'd, Cope 1892, Pl. XXII; Matthew 1916, fig. 3 and Pls. V-VI.

HORIZON AND LOCALITY.—Lance, South Dakota.

DIAGNOSIS.—Sole known species referred to the genus.

There is nothing to add to Matthew's detailed description of this specimen (1916, pp. 492-6). The morphology is well illustrated in Matthew's figure, here reproduced.

*Ectoconodon* Osborn 1898

1898. *Ectoconodon*, Osborn, *Bul. Amer. Mus. Nat. Hist.*, X, 171.

DEFINITION.—Upper molars relatively longer (anteroposteriorly) and narrower (transversely) than in *Didelphodon*, with style D more strongly developed and distinct, and with a very small median external cuspule somewhat internal to the outer edge of the styler shelf.

TYPE.—*E. petersoni* Osborn.

DISTRIBUTION.—Lance and equivalents, Wyoming and Montana.

This genus may be valid and does show definite differences from the type of *Didelphodon vorax*, but upon direct comparison these differences are less noteworthy than might be supposed, and the continued use of the name is provisional.

*Ectoconodon petersoni* Osborn 1898

1898. *E. petersoni*, Osborn, *Bul. Amer. Mus. Nat. Hist.*, X, 171.

LECTOTYPE.—Amer. Mus. No. 2223. Isolated upper molar. Fig'd, Osborn 1893, Pl. VIII, F (lower of two); 1898, fig. 1, F (lower); 1907, fig. 47, F (lower).

SYNTYPE.—Amer. Mus. No. 2224. Isolated upper molar. Fig'd, as above, upper figures.



HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

DIAGNOSIS.—Preferably used, *sensu lato*, for all members of the genus.

#### INCLUDED SPECIES

1927. *Ectoconodon montanensis*, Simpson, *Amer. Mus. Nov.*, No. 267, p. 5. Type: *Amer. Mus.* No. 14406, isolated left upper molar from Crooked Creek, Dawson County, Montana.

The larger and more distinctive of Osborn's syntypes is here made lectotype, since it is apparent that his two specimens do not fall within the ordinary range of a single species. *E. montanensis* Simpson is distinct and it will be necessary to use the name when the Hell Creek mammalian fauna is better known, but more mature consideration persuades the writer that the attempted separation of this species is not useful at the present time. There are thus at least three species in the genus, all included under *E. petersoni sens. lat.*

The trigon is like that of *Didelphodon vorax* save that the primary cusps are a little more pointed and the disparity between the lower pa and higher me is somewhat greater. The contour of the external shelf is almost identical, but the styles are rather different. A is even smaller. D, at best merely indicated in *Didelphodon*, is here a prominent cusp nearly as large as B and larger than the pa. The internal slope of D is long, and on it there is a small lesser tip just internal to the main one. The crest-like E is strongly marked. In addition there is a small cusp on the shelf between B and D and between the pa and me. It is very small and is connected by ridges to the latter two cusps, being considerably internal to the margin of the tooth.

Close comparison with *Didelphodon*, *Thlaeodon*, and *Pedionomys*, genera in which the orientation of the upper molars is certainly known, shows that Osborn's orientation of his isolated *Ectoconodon* teeth was in error,—both of his specimens are right upper molars, not left.

#### *Alphadon* Simpson 1927

1927. *Alphadon*, Simpson, *Amer. Jour. Sci.* (5) XIV, 125.

DEFINITION.—Didelphodontine upper molars. Styler cusps seen in *Didelphodon* less prominent than in that genus, but with a very strong median external cusp. Species of relatively small size.

This genus includes the smallest of the known didelphodontines. It seems to be rather sharply delimited and it differs more from the preceding three genera than do the latter among themselves.

#### *Alphadon marshi* Simpson 1927

1927. *A. marshi*, Simpson, *Amer. Jour. Sci.* (5) XIV, 125.

TYPE.—Y.P.M. No. 13659. Isolated upper molar.

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

DIAGNOSIS.—Sole species now referred to the genus.

The chief differences from *Ectoconodon* are in the relative development of the various styles. A and B are distinct and quite separate, B being the larger. D and B are about equal and are smaller than the pa or me. D is less conical than in *Ectoconodon* or *Thlaeodon*, and is elongated parallel to the edge. E is somewhat smaller. The most prominent outer cusp is median, cone-like, and rises from the cingulum shelf about halfway between the pa-me line and the outer border. It may be homologous with the very much smaller cusp in this region in *Ectoconodon*.

*Didelphodontine incertae sedis*  
"Superior molars, D" Osborn 1893

This type of upper molar is represented in the American Museum by Nos. 2221 and 2222 and in the Yale Museum by Nos. 13660 and 13661. The pr is higher than pa or me. Pl and ml are close to the pa and me and their sharp median edges, unlike those of *Pedionomys*, meet in a point. In the basin internal to this point are several small radiating ridges. Pa and me are about equal in size and are blunt. The external cingulum is narrow posteriorly but forms a spur anteriorly. From the circumstance that this spur is certainly anterior, it follows that these teeth are posterior upper molars, M<sup>4</sup>. They probably belong to the *Didelphodon-Thlaeodon-Ectoconodon* group.

## B. LOWER JAWS AND TEETH

Under this heading come two groups, closely related zoologically but quite distinct in the approach which they demand. On the one hand are two good lower jaws of *Eodelphis* from the Belly River of Alberta, one of *Euangelistes* from the Lance of Wyoming, and one of *Proteodidelphys* from the Variegated Sandstones (Areniscas abigarradas, grès bigarrés, *Proteodidelphys* beds of Ameghino) of Patagonia—the only positively identifiable South American mammal for which a pre-Tertiary age is at all probable. On the other hand are the numerous isolated teeth and small fragments of lower jaws from the Wyoming Lance. The former are amenable to the usual methods of paleontological revision and will be treated first. In dealing with the fragmentary Lance remains the more distinctive of the various morphological types of didelphid lower molars are described, but names are applied only to those which had already been named by Marsh. To attempt to name them all would serve no useful purpose at this time, and correlation with the upper molars described above is quite impossible at present.

*Eodelphis* Matthew 1916

1916. *Eodelphis*, Matthew, *Bul. Amer. Mus. Nat. Hist.*, XXV, 482.

DEFINITION.—Three lower incisors, the second enlarged, the others minute. No postcanine diastema. Anterior part of jaw deep and short. Trigonids of moderate height, wider than long, protoconid about equal in height to paraconid, metaconid smaller.

TYPE.—*E. cutleri* (Smith Woodward).

DISTRIBUTION.—Belly River beds, Alberta, Canada.

*Eodelphis cutleri* (Smith Woodward 1916)

May 30, 1916. *Cimolestes cutleri*, A. Smith Woodward, *Abst. Zool. Soc.*, London, No. 158; *Proc. Zool. Soc.*, London, 1916, p. 525.

July 24, 1926. *Eodelphis browni*, Matthew, *Bul. Amer. Mus. Nat. Hist.*, XXXV, 482.

1928. *Eodelphis cutleri*, Simpson, *Cat. Mes. Mam. Brit. Mus.*, p. 148.

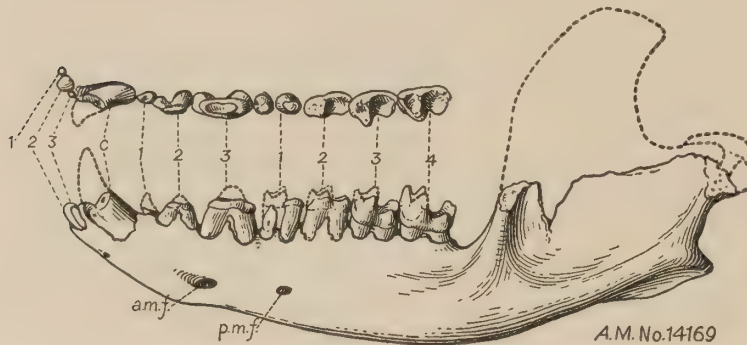


FIG. 48. *Eodelphis cutleri*, lower jaw, external view, and crown view of teeth, three halves natural size, No. 14169 *a.m.f.*, anterior mental foramen; *p.m.f.*, posterior mental foramen. (After Matthew, 1916.)

TYPE.—Brit. Mus. M11532. Most of dental portion of right lower jaw with crowns of  $P_3$  and  $M_{2-3}$ . Fig'd, Smith Woodward 1916, fig. 1; Simpson 1928B, Pl. XII, figs. 1-3.

TYPE OF *E. browni*.—Amer. Museum No. 14169. Most of left lower jaw, symphyseal region of right lower jaw, part of left zygoma, and much

of left temporal region. Fig'd, Matthew 1916, figs. 1-2 and Pls. II-IV.

HORIZON AND LOCALITY.—Belly River formation, Sand Creek, Red Deer River, Alberta.

DIAGNOSIS.—Sole known species of the genus. Length  $M_{1-4}$  about 18 mm.

The type of this species has recently been redescribed in detail by the writer (Simpson 1928B) and there is nothing to add to this account and the earlier one by Sir Arthur Smith Woodward (1916). The original reference to *Cimolestes* was largely on the basis of resemblance to "*Cimolestes*" *curtus*. Matthew erroneously states that the latter is the type of *Cimolestes* (Matthew 1916, p. 491), but, as will be shown below, it does not belong in that genus. He distinguishes *Eodelphis* as having a larger metaconid, longer and narrower heel with more distinct marginal cusps, and a higher internal and lower external border. The metaconid is, however, little if any larger. "*C.*" *curtus* originally had separate talonid cusps, but they are corroded in the type. The differences in proportions are slight and perhaps illusory, and the difference in height of the borders may be due in part at least to corrosion and wear. Smith Woodward states that the trigonid is less high in this species than in "*C.*" *curtus*, but this, also, is not clear. In fact it is impossible to establish any clear distinctions between these two genera, *Eodelphis* and *Diaphorodon*, but the latter is so little known and it is so very unlikely that a mammalian genus is really common to the Belly River and the Lance that they may properly be maintained as separate.



The so-called *Cimolestes cutleri* and *Eodelphis browni* were described almost simultaneously, each without knowledge of the other, and so were not originally contrasted. They are obviously very similar and are from the same formation and the same locality. The present writer has elsewhere suggested (1928B) that they are probably synonymous, recognizing, however, certain discrepancies in apparent molar structure which left the matter in doubt. There has since been discovered by C. M. Sternberg a third jaw, with the molars unusually well preserved, which seems to clear up the matter and indicate that these names are synonymous. This specimen, found since the present manuscript was complete, is being described elsewhere (Simpson, 1929C).

There is little to add to Matthew's description of the American Museum specimen and his figures are here reproduced. Matthew's statements that on  $M_3$  the paraconid and metaconid are of nearly equal height and the protoconid lower and that on  $M_4$  the paraconid is somewhat higher than the metaconid, the protoconid certainly lower than the paraconid and perhaps than the metaconid were based on a worn and broken specimen and now prove to be incorrect. The metaconid is distinctly smaller than the paraconid on all the molars, while the protoconid is about equal to the paraconid or a little higher.

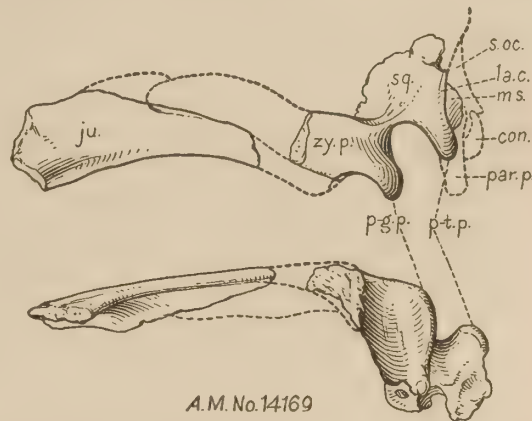


FIG. 49. *Eodelphis cutleri*, fragments of skull, side and under views, three halves natural size. The missing portions of the zygomatic arch and occipital region are partly restored in dotted outlines. Con., occipital condyle; la.c., lambdoidal crest; ju., jugal; ms., mastoid portion of periotic; par.p., paraoccipital process; p.-g.p., postglenoid process; p.-t.p., posttympanic process; s.oc., supraoccipital; sq., squamosal; zy.p., zygomatic process of squamosal. (After Matthew, 1916.)

### *Euangelistes* Simpson 1929

1929. *Euangelistes*, Simpson, *Ann. Carnegie Mus.*, XIX, 107.

DEFINITION.—A pediomyine of medium size. Molar trigonids elevated and sharply cut off from talonids. Trigonids compressed anteroposteriorly. Protoconids and metaconids subequal.  $M_1$  without trigonid basin, paraconid basal, vestigial.  $M_{2-4}$  with paraconids very small and progressively more median.

TYPE.—*E. petersoni* Simpson.

DISTRIBUTION.—Lance formation, Niobrara County, Wyoming.

### *Euangelistes petersoni* Simpson 1929

TYPE.—Carn. Mus. No. 11657. Left lower jaw with  $P_3$  and  $M_{1-4}$ . ( $M_4$  now said to be lost.)

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming.

DIAGNOSIS.—Sole identified species of the genus. Length  $M_{1-4}$ , 7.6 mm.  $P_3$ , 2.0 mm. Depth of ramus internally below  $M_4$ , 4.0 mm.

This is far the best preserved lower jaw yet found in the Lance and for that reason it demands taxonomic distinction. It probably belongs with some of the smaller upper teeth now referred, perforce, to *Pedionomys*. The molar type, with its lofty trigonids and very small paraconids, is a strange one for a didelphid and in habitus recalls rather some insectivores. The presence of four molars and the approximation of the entoconid and hypoconulid, among other things, clearly demand its inclusion in the didelphid group, however. The specimen has been fully described elsewhere (Simpson 1929B).

*Proteodidelphys* Ameghino 1898

1898. *Proteodidelphys*, Ameghino, *Rev. Sci.* (4) X, 74.

DEFINITION.—Four lower incisors, of nearly equal size. Premolars trenchant, increasing rapidly in size from anterior to posterior. Lengths of molars decreasing from  $M_1$  to  $M_3$ . Trigonid longer than broad. Protoconid somewhat higher than metaconid. Paraconid markedly smaller than either. Jaw stout. Incisive region anteroposterior.

TYPE.—*P. praecursor* Ameghino.

DISTRIBUTION.—Supposedly in the late Cretaceous of Patagonia.

As this is the only identifiable South American mammal which can possibly be regarded as of Mesozoic age, it is fitting that a few lines should be devoted to it here, although the present writer is dependent on the writings of Ameghino for his knowledge of the specimen. It is stated to be from the Chubutian or Variegated Sandstone formation of Patagonia, regarded by Ameghino as including the equivalents of the Neocomian and Aptian of Europe. This formation is now believed to belong somewhere in the late Cretaceous, and it may be approximately equivalent to the mammal-bearing horizons of the North American upper Cretaceous. It does not appear to be altogether certain, however, that *Proteodidelphys* is from these beds, especially in view of the mixture of fossils from different horizons which is now known to have occurred in some of Ameghino's other material. In his detailed description of the specimens (Ameghino 1900) he states that plants were found at one locality, dinosaurs at another, and four fragments of mammals at a third locality, not directly associated with any fossils indicative of true Cretaceous age. One fragment was identified as part of a movable plate of an armadillo, cf. *Peltephilus* and another as part of a caniniform tooth of a gravi-grade. These are not figured and the descriptions do not altogether allay suspicion that they might be reptilian. If correctly identified, they add to the evidence that these remains might be from a Tertiary pocket, for the presence of specialized dasypods and gravi-grades in the true Cretaceous would be quite extraordinary. A third specimen is a one-rooted tooth with an enameled crown worn in such a way as to be spatulate. Ameghino considered it as an incisor of a notoungulate and called it *Archaeoplus incipiens*. So far as one may judge from the figure and description, the tooth is probably but not surely mammalian and is otherwise indeterminate. *Proteodidelphys* itself is a didelphid, more primitive than any living form apparently, but not

more so than many early Tertiary species of *Peratherium* and not distinguished in any important way from some certainly Tertiary didelphids of Patagonia itself. Its molars do not show any of the remarkably various features which characterize the North American upper Cretaceous fauna, but are of the one type which survived into the Tertiary. Ameghino's figures do not compare at all closely with any Lance lower molars, although it is possible that comparison of the original would reveal a greater resemblance. In short, judged solely on its morphology, *Proteodidelphys* might well be of Cretaceous age, but could equally well, or even better, be placed in the lower Tertiary.

There is much indirect evidence indicative of a faunal continuity between North and South America in the upper Cretaceous. Until its age is exactly determined by further field work and discoveries, *Proteodidelphys* is too doubtful to add anything definite to this evidence and at the present time its importance, whether faunal or morphological, is slight. It is not necessary to review the fantastic phylogenies of Ameghino which make *Proteodidelphys* ancestral to most later mammals.

*Proteodidelphys praecursor* Ameghino 1898

1898. *P. praecursor*, Ameghino, *Rev. Sci.* (4) X, 74.

TYPE.—Right lower jaw, with all teeth and complete save for upper part of coronoid. Fig'd, Ameghino 1900, figs. 2-5.

HORIZON AND LOCALITY.—?Areniscas abigarradas, Patagonia. (Exact locality not published.)

DIAGNOSIS.—Sole species referred to the genus.

LANCE LOWER MOLARS

Morphological variations in this group are great. Most of them may apparently be broadly grouped under nine morphological types which are described below.

*Cimolestes* Marsh 1889 (Type 1)

1889. *Cimolestes*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 89.

DEFINITION.—Small Lance didelphid lower molars. Trigonid markedly higher than talonid.  $Pr^d$  larger than  $me^d$  and latter larger than  $pa^d$ .  $Pa^d$  strongly reduced.

TYPE.—*C. incisus* Marsh.

DISTRIBUTION.—Lance, Wyoming.

*Cimolestes incisus* Marsh 1889

1889. *C. incisus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 89.

TYPE.—Y.P.M. No. 11775. Isolated lower molar. Fig'd, Marsh 1889A, Pl. IV, figs. 12-15.

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming.

DIAGNOSIS.—Sole species now referred to the genus.



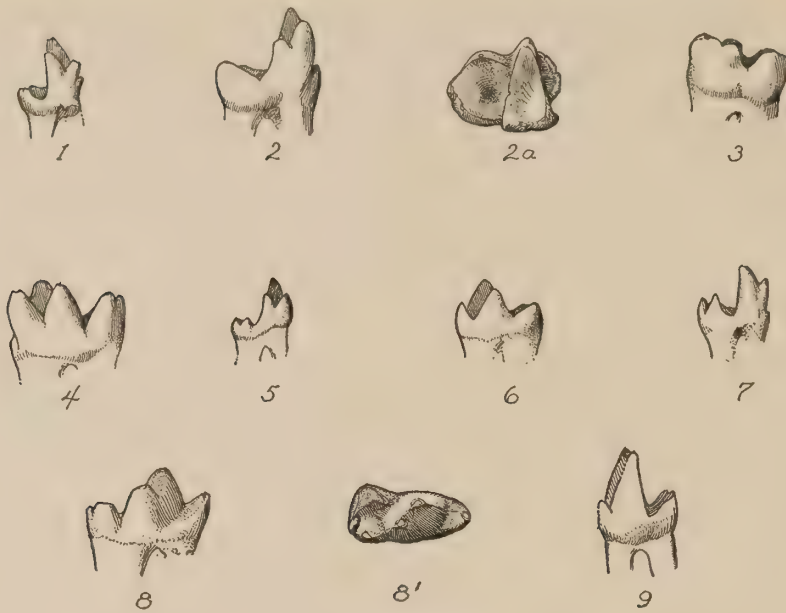


FIG. 50. Lower molars of Lance didelphids. 1, *Cimolestes*. 2, *Diaphorodon*. 3, "type 4." 4, *Delphodon*. 5, "type 5." 6, "type 6." 7, "type 7." 8, "type 8." 9, "type 9." 1-3,  $2\frac{1}{2}$  times natural size. 4-7, four times natural size. 8-9, five times natural size.

#### *Diaphorodon* Simpson 1927 (Type 2)

1927. *Diaphorodon*, Simpson, *Amer. Jour. Sci.* (5) XIV, 127.

DEFINITION.—Didelphid lower molars of relatively large size. Trigonid somewhat higher than talonid, compressed anteroposteriorly.  $Pr^d$  and  $pa^d$  nearly equal,  $me^d$  much reduced. Anterior cingulum broad, almost basined. Only two indefinite talonid cusps in type, but this probably due to corrosion as referred specimens show the normal didelphid arrangement.

TYPE.—*D. curtus* (Marsh).

DISTRIBUTION.—Lance, Wyoming.

This genus was necessarily erected for the reception of *Cimolestes curtus* Marsh which is certainly not congeneric with *Cimolestes incisus*. *Diaphorodon* is clearly related to *Eodelphis* of the Belly River and may be a direct descendant of the latter genus.

#### *Diaphorodon curtus* (Marsh 1889)

1889. *Cimolestes curtus*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 89.

1889. *Didelphodon ferox*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 88.

1927. *Diaphorodon curtus*, Simpson, *Amer. Jour. Sci.* (5) XIV, 127.

TYPE.—Y.P.M. No. 11774. Isolated lower molar. Fig'd, Marsh 1889A, Pl. IV, figs. 8-11.

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming.

DIAGNOSIS.—Sole recognized species of the genus.

*Didelphodon ferox* was based on a badly worn and broken lower molar (Y.P.M. No. 11828) which appears to be conspecific with the type of *D. curtus*. *Didelphodon ferox* was published a page previous to *Cimolestes curtus*, but the latter name is retained as the former was based on an inadequate type.

### *Delphodon* Simpson 1927 (Type 3)

1927. *Delphodon*, Simpson, *Amer. Jour. Sci.* (5) XIV, 127.

DEFINITION.—Trigonid little higher than talonid.  $Pa^d$  and  $me^d$  nearly equal,  $pr^d$  equal or slightly higher. Talonid large and basined, with three well defined cusps.  $Hl^d$  and  $en^d$  approximated. Anterior cingulum not prominent, not basined.

TYPE.—*D. comptus* (Marsh).

DISTRIBUTION.—Lance, Wyoming.

A great many teeth, with considerable range in size and some variation in proportions, fall under this genus, taken broadly. It certainly includes several species of lower molars and possibly more than one natural genus. Its relative abundance, variation, and generalized character suggest that this genus includes the lower teeth originally associated with the uppers referred to *Pediomys*, *sensu lato*. At the same time, this association is not proven and the type species is certainly not congeneric with *Didelphodon ferox* Marsh and can hardly have belonged with *Didelphodon vorax*, the genotype. To avoid incorrect association, it has therefore been necessary to erect a new genus for Marsh's species, and it is also convenient to have a name which may properly designate these most common of Lance lower molars. Since this memoir was completed, Russell (1928) has given the name ?*Delphodon praenuntius* to one sort of teeth of this group. The holotype is 4.6 mm. in length and has the  $pa^d$  and  $me^d$  close together. Many such names could be proposed for the varied teeth of this type.

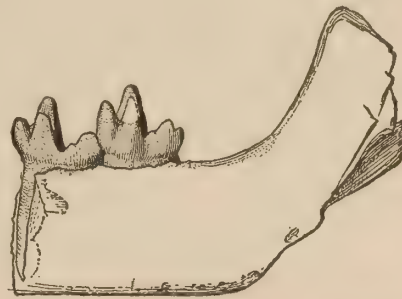


FIG. 51. Lance pediomyine. Fragment of right lower jaw with two molars. Y.P.M. No. 10685.

### Type 4

Trigonid little higher than talonid.  $Pr^d$  and  $me^d$  nearly equal,  $pa^d$  higher. Three talonid cusps, but  $hl^d$  and  $en^d$  imperfectly separated. Large.

This is close to *Diaphorodon* and may represent a different part of the dentition of that genus. The chief difference is in the markedly lower protoconid.

### Type 5

Trigonid higher than talonid.  $Pr^d$  much the highest cusp.  $Pa^d$  and  $me^d$  subequal. Talonid strongly marked off from trigonid. Very small.



FIG. 52. Lance pediomysine. Fragment of left lower jaw with two premolars. Y.P.M. No. 10693. Five times natural size.

#### TYPE 6

Trigonid and talonid nearly equal in height.  $Pr^d$  higher than  $me^d$  and  $me^d$  than  $pa^d$ . Anterior cingulum absent.

The absence of the anterior cingulum is remarkable in this fauna.

#### TYPE 7

Trigonid somewhat higher than talonid.  $Pr^d$  slightly higher than  $me^d$ .  $Pa^d$  much reduced. Talonid cusps unusually distinct from each other and sharp.

#### TYPE 8

Trigonid little higher than talonid, compressed transversely, much longer than broad.  $Pr^d$  higher than  $me^d$  and latter higher than  $pa^d$ .

This is the type of lower molar associated by Osborn with his *Synconodon* (see below). It is somewhat doubtful to what extent the essential character, the lateral compression, is of taxonomic value and whether it is not rather due to position in the series. The teeth have all the characters of the milk molars of modern opossums.

#### TYPE 9

Trigonid higher than talonid.  $Pr^d$  and  $me^d$  about equal.  $Pa^d$  almost vestigial. Two very distinct talonid cusps.

### C. DOUBTFUL OR INVALID FORMS

It is convenient to gather here several supposed Cretaceous mammals, whether based on upper or lower teeth, the status of which is dubious.

#### *Boreodon* Lambe

1902. *Boreodon*, Lambe, *Con. Can. Pale.*, III, 79.

SPECIES.—*B. matutinus* Lambe, genotype, loc. cit. Type: a single premolar from the Belly River, Red Deer River, Alberta.

DESCRIPTION.—“The crown is in the form of a laterally compressed cone, somewhat rounded above, angular in front, evenly rounded behind, with a well defined, undulating cingulum encircling its base. A slight lateral concavity, more clearly defined within, occurs on each side of the tooth near the base of the crown in line with the cleft between the roots. The cingulum is angular and prominent at either end, becoming rounded and broader on the sides.”

This form was referred to the Multituberculata by Lambe but this was certainly incorrect, as Matthew (1916) has remarked. It is probably the premolar of a didelphid, but is indeterminate.



*Stagodon* Marsh

1889. *Stagodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 178.

SPECIES.—*Stagodon nitor*, Marsh 1889, loc. cit., genotype. Type: a single premolar from the Lance of Niobrara County, Wyoming.

*Stagodon tumidus*, Marsh 1889, loc. cit. Type: a single premolar from the Lance of Niobrara County, Wyoming.

*Stagodon validus*, Marsh 1892, *Amer. Jour. Sci.* (3) XLIII, 256. Type: anterior part of right lower jaw with crown of P<sub>3</sub>.

DESCRIPTION.—“[In *S. nitor*] the striking character of all the molar teeth secured is the resemblance of their crowns to a drop of viscous fluid. . . .” “[*S. validus*] shows alveoles for three incisors closely crowded together, the first, or inner one, being much the largest. A very stout canine . . . was present, and behind it, in close contact, follow two premolars, the second being much the larger. These are both much worn, but the surface of the crowns preserved is coarsely striate or rugose. . . .”

*Stagodon* includes only premolars of Didelphodontinae, and is undoubtedly synonymous in whole or in part with *Didelphodon*, *Thlaeodon*, or *Ectoconodon*. Complete cheek series of these and of any other genera which may occur would be necessary to elucidate the true synonymy, and in any event it would seem unwise and unnecessary to replace any of the names based on molars by *Stagodon*, based on material which is generically uncharacteristic.

*Dryolestes tenax* Marsh 1889

1889. *D. tenax*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 87.

TYPE.—Y.P.M. No. 10698, lower jaw without teeth.

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

The type jaw is a small didelphid and has nothing to do with the Jurassic genus *Dryolestes*. Otherwise it is indeterminate and the name a *nomen nudum*.

*Platacodon* Marsh

1889. *Platacodon*, Marsh, *Amer. Jour. Sci.* (3) XXXVIII, 178.

SPECIES.—*P. nanus*, Marsh 1889, loc. cit., genotype. Three teeth from the Lance of Niobrara County, Wyoming.

Hatcher (1900) has adduced evidence that these are fish teeth and not mammalian, a possibility which Marsh recognized.

*Synconodon* Osborn 1898

1898. *Synconodon*, Osborn, *Bul. Amer. Mus. Nat. Hist.*, X, 171.

SPECIES.—*S. sexcusps*, Osborn 1898, loc. cit., genotype. Syntypes: A. M. Nos. 2218, 2220, isolated upper and lower molars, from the Lance of Niobrara County, Wyoming.

As intimated above (lower molars, type 8) it is very probable that the lower molars of this sort are deciduous teeth of one of the more usual didelphids. The upper molar syntype has been mislaid or lost, an ordinary small *Pedionomys* upper molar now being preserved under this number. Search of the extensive Yale, American Museum, and National Museum collections failed to reveal another like it except one which is broken,—a first upper molar or deciduous upper molar of *Pedionomys*, *sens. lat.*, with the cingulum broken off. Such imperfections are very difficult to observe, especially without the aid of a binocular, and in the absence of the original some suspicion must remain that this was the character of the upper tooth figured by Osborn. If this is not the case and Osborn's view is confirmed by further discoveries, *Synconodon* is entirely unlike anything else known and is a very novel element of uncertain affinities in the Lance fauna.

*Archaeoplus* Ameghino 1898

1898. *Archaeoplus*, Ameghino, *Sin. Geol. Pal., Seg. Cen. Nac.*, I, 174.

SPECIES.—*A. incipiens*, Ameghino 1898, loc. cit., genotype. Type: a supposed incisor.

This form, of wholly doubtful age and affinities, has already been discussed in dealing with *Proteodidelphys* above.

“*Telacodon*” *praestans* Marsh 1892

1892. *T. praestans*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 258.

TYPE.—U.S.N.M. No. 2133. Fragment of lower jaw with two molars. Fig'd, Marsh 1892A, Pl. IX, fig. 4.

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming.

There is no positive basis for referring this species to *Telacodon*, as the type is not directly comparable with the genoholotype. Such reference is not impossible, but the morphology of the teeth suggests that they are rather the lower molars of a didelphid and the species is of very doubtful status.

## ORDER INSECTIVORA Gray 1827

Under this heading three Lance genera are to be discussed, *Gypsonictops*, *Telacodon*, and *Batodon*. None of these is well known, *Gypsonictops* resting on isolated upper teeth, P<sup>4</sup> to M<sup>3</sup>, and the other two each on the anterior part of a lower jaw. *Gypsonictops* is of considerable importance as it seems to prove that there is a minor placental element in the dominantly multituberculate-marsupial Lance fauna. The other two are also probably placental, but the evidence is less clear. Their reference to the Insectivora does not rest on any tangible ordinal characters subject to definition, but on resemblances to later mammals, difficult of formal recognition but sufficiently definite to justify this allocation even aside from theoretical considerations. *Gypsonic-*

*tops* apparently belongs either in the Zalambalestidae or in the Leptictidae, but any attempt to refer the other two genera definitely to some known family would probably be premature.

*Gypsonictops* Simpson 1927

1927. *Gypsonictops*, Simpson, *Amer. Mus. Novitates*, No. 267, p. 6.

DEFINITION.—Typical upper molars of leptictid type, short, transverse, with crescentic protocone, laterally compressed paracone and metacone, small para- and metaconules, narrow, sharp external cingulum, a small heel posterior to the protocone, and a feeble anterior cingulum. Referred last molar oblique, metacone reduced, para-style large and prominent. Referred last premolar with paracone and metacone closely approximated, the former the larger, protocone a small low heel directly internal to the metacone, with small posterointernal cingulum but no anterointernal cingulum.

TYPE.—*G. hypoconus* Simpson.

DISTRIBUTION.—Lance and equivalents, Wyoming and Montana.

Last upper premolars and typical upper molars of this type were known to Marsh, who referred them to *Telacodon laevis* and *Batodon tenuis* (1892A, Pl. IX, fig. 2, Pl. XI, figs. 1-2). Since the types of the latter genera and species have no parts directly comparable with these upper teeth, such association is not open to proof. It may eventually prove that *Gypsonictops* is the upper dentition of one or the other of these two genera, but the association would indicate an animal quite different from those which *Gypsonictops* seems most closely to resemble in the upper cheek teeth and in any event this important type, the only definite American pre-Paleocene placental, should have an applicable name.

In molar structure *Gypsonictops* stands very close to the Paleocene to Oligocene Leptictidae. If  $P^4$  is correctly identified it is distinguished from that of any later leptictid by being somewhat less molariform, a primitive feature. If, as is possible, this tooth is really  $P^3$ , then it is somewhat more advanced than in the later forms, which is improbable. There is also a close resemblance to *Zalambdalestes* of the Mongolian Cretaceous, although *Gypsonictops* is more advanced in the possession of a definite hypocone. Reference to one or the other of the closely related families Leptictidae and Zalambdalestidae would depend chiefly on the specializations shown by the more anterior teeth, as yet unknown in association. For the present provisional reference to the Leptictidae is possible, and in any event relationship to this division of the Insectivora is clearly indicated.

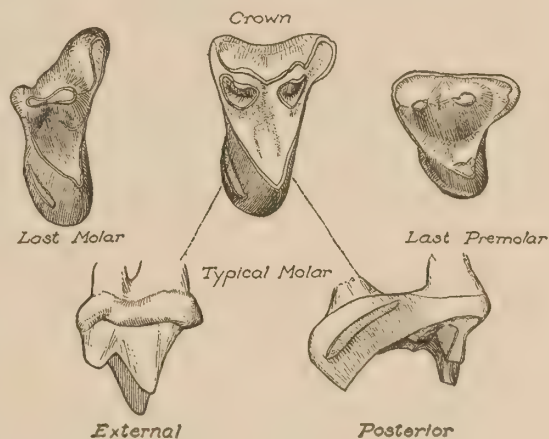


FIG. 53. *Gypsonictops hypoconus*. Upper cheek teeth. Eight times natural size.



*Gypsonictops hypoconus* Simpson 1927

1927. *G. hypoconus*, Simpson, *Amer. Mus. Novitates*, No. 267, p. 6.

TYPE.—Y.P.M. No. 13662. Isolated upper molar.

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming. Referred specimens from Hell Creek beds of Montana.

DIAGNOSIS.—Sole known species of the genus.

*Telacodon* Marsh 1892

1892. *Telacodon*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 258.



FIG. 54. *Telacodon laevis*. Part of right lower jaw with last three premolars, external view, type. Ten times natural size.

DEFINITION.—Four premolars, simple, trenchant, the last much the largest. Canine present but small. A much enlarged incisor, procumbent, with root extending back beneath the canine.

TYPE.—*T. laevis* Marsh.

DISTRIBUTION.—Lance, Wyoming.

It is uncertain whether *T. praestans* Marsh, treated on a previous page, can be referred to this genus.

*Telacodon laevis* Marsh 1892

1892. *T. laevis*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 258.

TYPE.—Y.P.M. No. 11780. Anterior part of lower jaw with P<sub>2-4</sub>. Fig'd, Marsh 1892A, Pl. IX, fig. 3.

HORIZON AND LOCALITY.—Lance, Niobrara County, Wyoming.

DIAGNOSIS.—Sole species in which the parts shown by the type are known.

Marsh believed that the alveoli anterior to the teeth preserved were for two more premolars, making five in all, and a large procumbent canine. This interpretation does not appear to be sustained by the present study. Anterior to the preserved teeth is an alveolus for another premolar, the first, a very small tooth with a larger anterior and shorter posterior root, very close together. The alveolus anterior to this one is wider than any which follow and is quite undivided. It apparently lodged a small canine. The large anterior alveolus, extending back beneath the canine, must have been for an enlarged, procumbent incisor.

*Batodon* Marsh 1892

1892. *Batodon*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 258.

DEFINITION.—Premolars simple, trenchant, three or, more probably, four in number. Three teeth preserved in genoholotype preceded by a small alveolus, for P<sub>1</sub> or a

vestigial canine, and this preceded by a large procumbent tooth, a large canine or incisor.

TYPE.—*B. tenuis* Marsh.

DISTRIBUTION.—Lance, Wyoming.

This genus appears to be similar to, but not identical with *Telacodon*. It is not didelphid, for if there were only three premolars the canine was vestigial and one of the incisors was hypertrophied. This would suggest the caenolestoids, but the specimen is so doubtful that such speculation has no value whatever. It is more probable, and less sensational, that it is a small insectivore.

Marsh considered the large procumbent tooth as the canine and the small alveolus as for  $P_1$ , and this seems the more probable of the two possible interpretations.



U.S.N.M. 2139

FIG. 55. *Batodon tenuis*. Part of left lower jaw, external view, type. Five times natural size.

*Batodon tenuis* Marsh 1892

1892. *B. tenuis*, Marsh, *Amer. Jour. Sci.* (3) XLIII, 258.

TYPE.—U.S.N.M. No. 2139. Anterior part of lower jaw with canine (or enlarged incisor) and three premolars. Fig'd, Marsh 1892A, Pl. XI, fig. 5.

HORIZON AND LOCALITY.—Lance formation, Niobrara County, Wyoming.

DIAGNOSIS.—Sole species of the genus.

### III. PHYLOGENY AND RELATIONSHIPS

Six orders of mammals are known to have lived in the Mesozoic:

1. Multituberculata, Triassic to Eocene.
2. Triconodonta, Jurassic.
3. Symmetrodonta, Jurassic.
4. Pantotheria, Jurassic.
5. Marsupialia, Cretaceous to Recent.
6. Insectivora, Cretaceous to Recent.

Since the first Mesozoic mammal was discovered to the present day, there has never been any real agreement among students as to the relationships of these various

orders among themselves or to later mammals, or even as to the real existence of the various groups as such. This lack of any approach toward unanimity, even as regards the very fundamentals of the whole problem, has been partly due to the faulty nature of the known materials. The inadequacy of knowledge has been so deeply felt that, in general, students of mammals, aside from two or three specialists, have not even felt it necessary to attempt to grasp the true scope and meaning of what has been known. Attention has chiefly been focused on the last third of mammalian history without troubling the obscurity of the first two thirds.

This memoir and its companion volume (Simpson 1928B) should show, however, how much more extensive our knowledge really is than would be supposed after a perusal of any general works on mammals, recent or fossil. The specimens at our disposal could be increased a thousand-fold and still fail to

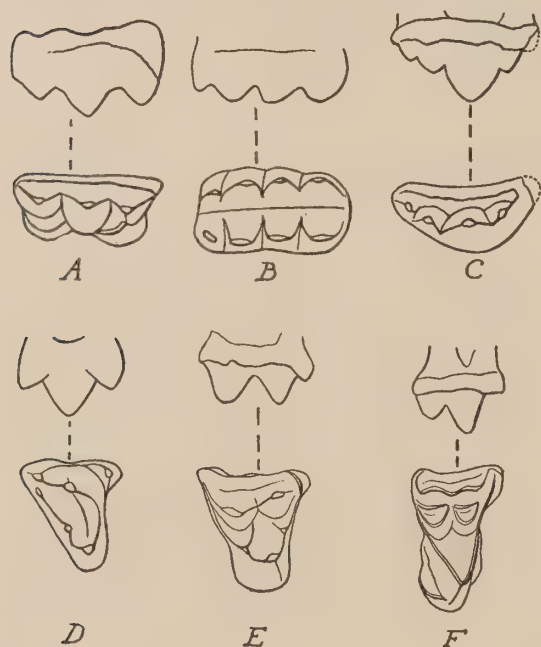


FIG. 56. Upper molars in the six Mesozoic orders of mammals. A, Triconodonta, *Priacodon*. B, Multituberculata, *Ctenacodon*. C, Symmetrodonta, *Eurylambda*. D, Pantotheria, *Melanodon*. E, Marsupialia, *Pedimys*. F, Insectivora, *Gypsonictops*. Not to scale.



give definitive answers to all the problems which turn on them, and anything done now will inevitably be changed, perhaps very radically changed, by future discoveries, but the time is ripe for the formation of new working hypotheses as to relationships, and the material is adequate for the formation of such hypotheses, provided that they are based not on one collection or another and not on one aspect and approach or another, but on the whole of the material considered from as many points of view as lie within the powers of the worker.

After studying all the known material, the present writer attempted an interpretation of the affinities of the various groups of Mesozoic mammals. In the *Catalogue of Mesozoic Mammals in the British Museum* the Triassic and Jurassic mammals have been treated in some detail in this connection, and in formulating the working hypotheses there expressed all of the facts published here were also taken into consideration. The multituberculates have been further considered elsewhere by Granger and Simpson (1929), and the more important Mesozoic insectivores by Gregory and Simpson (Gregory and Simpson 1926A, Simpson 1928C). It is not necessary to repeat all the arguments and all the bases for the tentative conclusions thus reached. The present section therefore is confined to a brief consideration of the Mesozoic marsupials and to a still more brief *résumé* of present views as to the probable phylogeny and relationships of all the Mesozoic mammals.

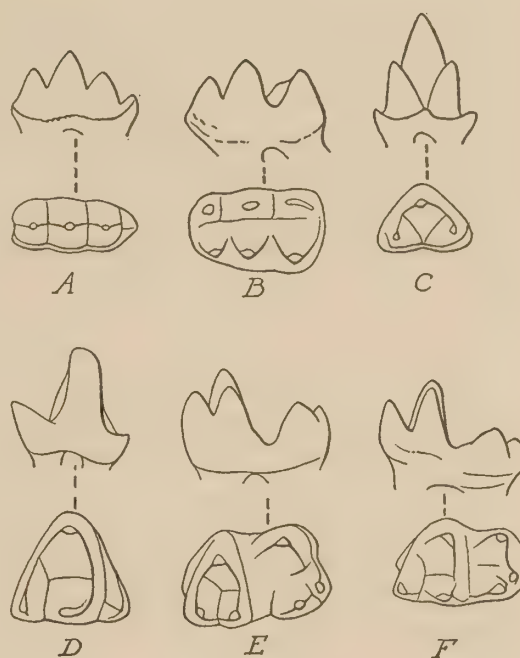


FIG. 57. Lower molars of Mesozoic mammals. A, Triconodonta, *Priacodon*. B, Multituberculata, *Ctenacodon*. C, Symmetrodonta, *Tinodon*. D, Pantotheria, *Dryolestes*. E-F, Marsupialia, Lance didelphids. Not to scale.

## THE MESOZOIC MARSUPIALS

The earliest known marsupial is *Eodelphis* from the Belly River, upper Cretaceous. Many of the Triassic and Jurassic mammals have been believed already to have been definite marsupials, but in any just conception of taxonomy a mammal is not to be classified as a marsupial merely because it is ancient or primitive but only because it has characters which taken together characterize the Marsupialia and no other group. Reëxamination of the Triassic and Jurassic mammals has shown beyond apparent question that none of them does show such characters. No mammals earlier than the Cretaceous can reasonably be referred to the Marsupialia except on purely theoretical

grounds in opposition to what is actually known at present. *Eodelphis* and the numerous Lance didelphids, on the contrary, while very primitive in many respects, already show the fundamental special marsupial characters in the known parts as clearly as does any recent member of the group. In the upper Cretaceous, marsupials and placentals were both in existence and were clearly marked off from each other. There is no actual paleontological evidence that one group is older than the other or that one group was derived from the other. There is evidence, both from comparative anatomy and from paleontology, that marsupials and placentals were derived from a common stock, but the actual record of this divergence is wholly lacking. Presumably it is to be sought in the great interval, still almost blank so far as mammals are concerned, between the middle or upper Jurassic and Belly River or Djadokhta time.

It is reassuring to find that the first members of the marsupial line (and the same is true of the first placentals) clearly belong to a stock which has long been adjudged on other evidence to be the most primitive of its subclass. They are opossums, using the term in a broad sense. At the present time the opossums, although occupying fairly diverse habitats, are almost stereotyped in form. Were they known chiefly from their teeth, as are their Cretaceous allies, they could hardly be placed in more than one genus. They may, as Thomas has supposed, be undergoing an expansion and radiation, but if so it is a radiation of limited scope or in its very first stages. In the Cretaceous, on the contrary, the primitive marsupials grouped around the didelphid stem were apparently in a racial phase when they were varying greatly and expanding into various modes of life, that is, actively radiating. Even in our limited uppermost Cretaceous collections from a single faunal facies the range in morphology and in type of adaptation is clearly great. Such types as *Thlaeodon* on the one hand and *Nyssodon* on the other represent wide extremes for a single stock not then very ancient. Along with these more extreme types are found others which differ hardly at all in adaptation and very little in morphology from the recent *Didelphis*. From this diverse group at the base of the marsupial order the increasingly specialized lines culminating in the peculiar forms of the South American Tertiary and the Australian Pleistocene and Holocene were probably derived. As has always been the case in the early stages of differentiation of a mammalian stock, the majority of these potential lines of radiation were undoubtedly sterile. This was certainly true in North America, where only the most central and primitive phylum survived the crucial time of the close of the Cretaceous period. The later opossums, *Peratherium* and its probable descendant *Didelphis*, represent only the least specialized of the didelphid races which occupied this continent in the later Cretaceous.

## RÉSUMÉ OF ORDINAL RELATIONSHIPS

As with the small group of the didelphids, so it has apparently always been with larger groups as well. When an order, a subclass, or a class first has its origin and begins its expansion it breaks up gradually into a number of diversified stocks. After a time these are weeded out and only a limited number of them survive to undergo the



same process of diversification and selection on a smaller scale. The unsuccessful or only temporarily successful lines become extinct and only their fossil remains are found to puzzle the taxonomist. They will not enter into the divisions of classifications based, as classifications almost always have been, only on the much better known surviving lines. Within the subclass Eutheria this is clearly seen in the Paleocene and Eocene mammals. In addition to the various groups which are ancestral to later mammals and which are relatively easy to classify in our present system, there are others which can only be characterized as aberrant and extinct side lines—aberrant, usually, only in the sense that they differ from the more successful and more familiar phyla.

This apparently was equally true of the whole class in its early history. Of the four major groups in the Jurassic,—Multituberculata, Triconodonta, Symmetrodonta, and Pantotheria,—only one, the Pantotheria, shows evidence of having any significance in regard to Tertiary mammals. This order (in a broad sense, not necessarily any actually known family or genus) was the only potentially successful and fruitful Jurassic group and was destined to give rise to most or all recent mammals (save monotremes).

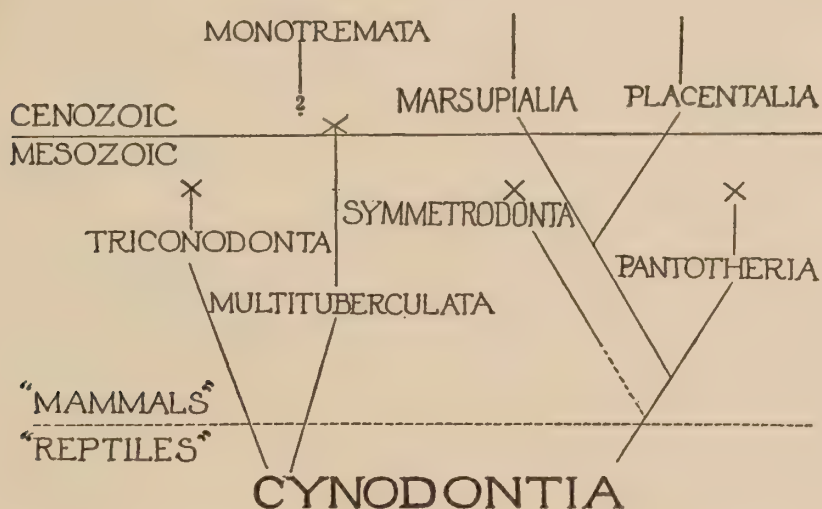


FIG. 58. Suggested relationships of the major groups of mammals.

The multituberculates were independently derived from the ultimate mammalian common ancestry, probably within a group which must be called reptilian by definition. They had their own great and eventful history throughout the Mesozoic and Paleocene and even into the true Eocene, but they then became extinct. They are relatively well known and it is justifiable to place them in a distinctive subclass, the Allotheria.

The triconodonts represent another early side line, probably of equally remote derivation and equally independent of other mammals. Their history, while not short even in comparison with a number of Tertiary orders, was more limited and less event-



ful than that of the Multituberculata. So far as now known, they became extinct at the end of the Jurassic.

The symmetrodonts are very imperfectly known. It seems a reasonable view at present that they were a sterile offshoot from near the base of the pantotherian line.

In the upper Cretaceous, when next a real glimpse of mammalian life is afforded, nothing remains of the triconodonts or symmetrodonts. The multituberculates survive in changed form but are nearing the end of their history. The two great groups of Tertiary and recent mammals, the Marsupialia and Placentalia, appear for the first time and are probably both derived from the general pantotherian stock of the Jurassic. The post-Mesozoic history of the Mammalia is almost wholly concerned with the later development of these two groups.

These views are tentatively summed up in Fig. 58.

## IV. DISTRIBUTION

### *AMERICAN FAUNAL LISTS*

THE faunas included in the primarily zoölogical and morphological treatment on the preceding pages are here separated into formal lists for each horizon and locality. Names considered very doubtful or positively invalid are omitted and all are used in the same sense as in the morphological section. Thus the fauna of the Lance is actually richer and more varied than its faunal list would seem to indicate.

### JURASSIC

MORRISON FORMATION, COMO BLUFF, WYOMING. (QUARRY 9.)

#### MULTITUBERCULATA:

*Ctenacodon serratus*

*C. scindens*

*C. laticeps*

*Psalodon potens*

*P. fortis*

?*P. marshi*

#### TRICONODONTA:

*Phascolodon gidleyi*

*Aploconodon comoënsis*

*Trioracodon bisulcus*

*Priacodon ferox*

*P. robustus*

*P. lulli*

*P. grandaevus*

#### SYMMETRODONTA:

*Tinodon bellus*

*T. lepidus*

*Amphidon superstes*

*Eurylambda aequicrurius*

#### PANTOTHERIA:

*Paurodon valens*

*Archaeotrigon brevimaxillus*

*A. distagmus*

*Tathiodon agilis*

*Dryolestes priscus*

*Laolestes eminens*  
*L. grandis*  
*Amblotherium gracilis*  
*A. debilis*  
*Herpetairus arcuatus*  
 ?*H. humilis*  
*Melanodon oweni*  
*M. goodrichi*  
*Euthlastus cordiformis*  
*Miccylyotyrans minimus*  
*Malthacolestes osborni*  
*Pelicoptysis dubius*  
*Docodon victor*  
*D. striatus*  
*D. crassus*  
*D. affinis*  
*D. superus*

MORRISON FORMATION, GARDEN PARK, COLORADO

PANTOTHERIA:

*Kepolestes coloradensis*  
*Docodon* sp.

CRETACEOUS

BELLY RIVER FORMATION, RED DEER RIVER, ALBERTA

MULTITUBERCULATA:

*Cimolomys primaevus*

MARSUPIALIA:

*Eodelphis cutleri*

EDMONTON FORMATION, ALBERTA

MARSUPIALIA:

cf. *Diaphorodon* sp.

LANCE FORMATION, NIOBRARA COUNTY, WYOMING

MULTITUBERCULATA:

*Meniscoëssus robustus*

*Meniscoëssus* spp. -

*Cimolomys gracilis*

*Cimolomys* spp.

MARSUPIALIA:

*Pediomys elegans*

*Pediomys* spp.



*Pediomys hatcheri*  
*Nyssodon punctidens*  
*Didelphodon vorax*  
*Ectoconodon petersoni*  
*Ectoconodon* sp.  
*Alphadon marshi*  
*Alphadon* spp.  
*Euangelistes petersoni*  
*Cimolestes incisus*  
*Diaphorodon curtus*  
*Delphodon comptus*  
 Gen. et spp. indet.

## INSECTIVORA:

*Gypsonictops hypoconus*

## ?INSECTIVORA inc. sed.:

*Batodon tenuis*  
*Telacodon laevis*

## LANCE FORMATION, SOUTH DAKOTA

## MULTITUBERCULATA:

*Meniscoëssus conquistus*

## MARSUPIALIA:

*Thlaeodon padanicus*

## HELL CREEK FORMATION, CROOKED CREEK, DAWSON COUNTY, MONTANA

## MULTITUBERCULATA:

*Essonodon browni*  
*Meniscoëssus borealis*  
*Cimolomys* spp.

## MARSUPIALIA:

*Ectoconodon montanensis*  
*Pediomys* sp.  
*Didelphodontinae* indet.

## VICINITY OF FORSYTH AND SNOW CREEK, MONTANA

## MULTITUBERCULATA:

*Meniscoëssus borealis*  
*Cimolomys* sp.

## MARSUPIALIA:

*Thlaeodon* sp.

## INSECTIVORA:

*Gypsonictops hypoconus*

## *WORLD CORRELATION AND DISTRIBUTION*

ONE or more specimens of Mesozoic mammals are now known from each of the following localities and horizons in the world:

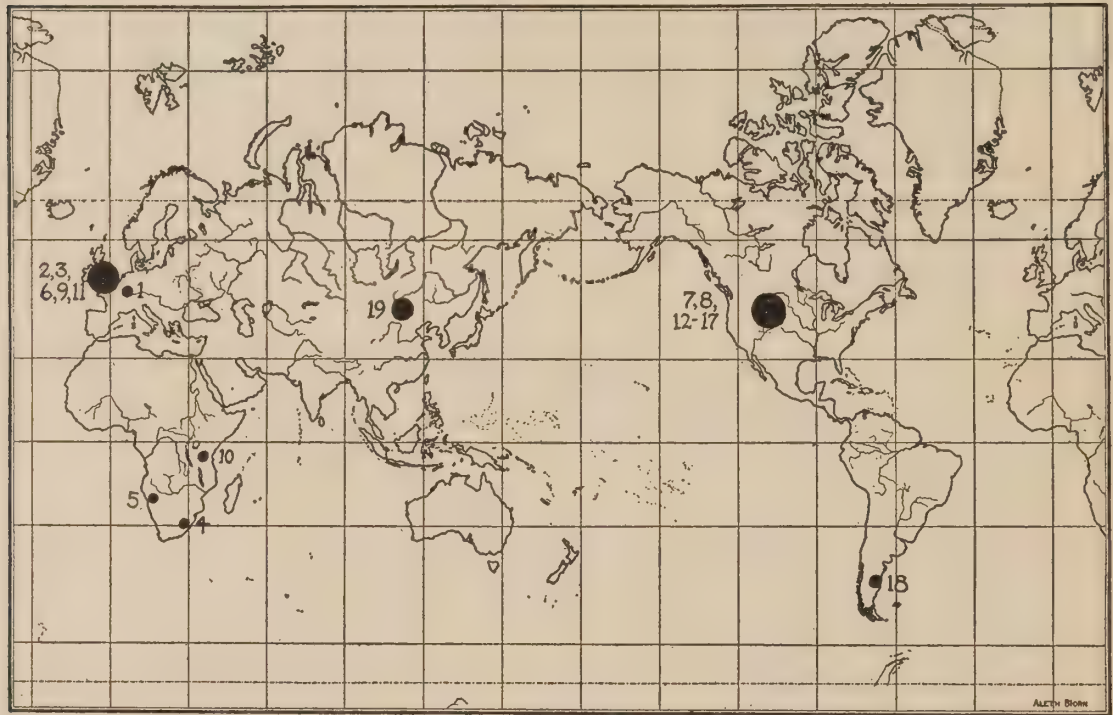


FIG. 59. Known occurrences of Mesozoic mammals. The numbers correspond to those in the text.  
Base, zoögeographic chart from The American Museum of Natural History.

### RHAETIC OR LOWEST LIASSIC

1. Württemberg, Germany. (Several localities in same region.)
2. Watchet, Somersetshire, England.
3. Holwell, Somersetshire, England.
4. Basutoland, South Africa.
5. Kaokofeld, Southwest Africa.

### MIDDLE JURASSIC

6. Stonesfield, Oxfordshire, England.

## UPPERMOST JURASSIC

7. Como Bluff, Wyoming, U.S.A.
8. Garden Park, Colorado, U.S.A.
9. Durdlestone Bay, Dorsetshire, England.
10. Tendaguru, Tanganyika Territory, Africa.

## LOWEST CRETACEOUS (WEALDEN)

11. Hastings, Sussex, England.

## UPPER CRETACEOUS (BELLY RIVER)

12. Red Deer River, Alberta, Canada.

## UPPER CRETACEOUS (EDMONTON)

13. Red Deer River, Alberta, Canada.

## LATEST CRETACEOUS (LANCE AND HELL CREEK)

14. Niobrara County, Wyoming, U.S.A.
15. Crooked Creek, Dawson County, Montana, U.S.A.
16. Vicinity of Forsyth and Snow Creek, Montana, U.S.A.
17. South Dakota, U.S.A. (Exact locality uncertain.)

## ?CRETACEOUS

18. Chubut, Patagonia, Argentina.

UPPER CRETACEOUS  
(DJADOKHTA)

19. Shabarakh Usu, Mongolia.

This list of localities is not very imposing, considering the vast span of time which it includes, and even so it is somewhat misleading, as several of the localities have furnished only one or two specimens and only four or five have furnished anything like a fauna in any true sense of the word.

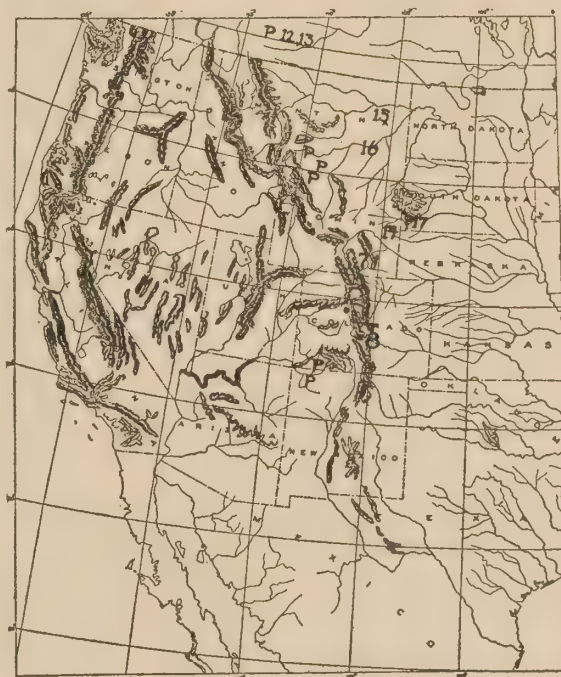


FIG. 60. Known occurrences of Mesozoic mammals in North America. P indicates the more important Paleocene localities. The numbers correspond to those in the text. Base, zoögeographic chart from The American Museum of Natural History.



AGE	N. AMERICA	S. AMERICA	EUROPE	AFRICA	ASIA
PALEOCENE	TIFFANY <i>Echypodus</i>	18 } CHUBUT 14-17 13 12 EDMONTON BELLY RIVER	CERNAYSIAN <i>Neoplagiaulax</i>		GASHATO <i>Prionessus</i>
	TORREJON <i>Ptilodus</i>				
	PUERCO <i>Polymastodon</i>				
CRETACEOUS	LANCE <i>Dipriodon</i>				
				19 } DJADOCHTA <i>Djadochtatherium</i>	
JURASSIC	MORRISON <i>Ctenacodon</i>	7-8	11 } WEALDEN <i>Loxaulax</i> 9 } PURBECK <i>Plagiaulax</i> 6 } STONESFIELD <i>Stereognathus</i>	TENDAGURU 10	
TRIASSIC		1-3		STORMBERG <i>Tritylodon</i>	4-5

FIG. 61. Tentative correlation of the mammal-bearing formations of the Mesozoic and of the principal Paleocene mammal horizons. The numbers correspond to those in the text.

Upper Cretaceous mammals are known only from North America, Asia, and possibly South America. They provide no real comparisons between these continents and no opportunity for precise correlation. The known genera and approximate correlation of the Triassic and Jurassic mammalian faunas are summed up in the following table:

LATEST JURASSIC	NORTH AMERICA	EUROPE	AFRICA
	<i>Ctenacodon</i> ————	<i>Ctenacodon</i>	
	<i>Psalodon</i>	<i>Plagiaulax</i> <i>Bolodon</i>	
	<i>Phascolodon</i>		
	<i>Aploconodon</i>		
	<i>Trioracodon</i> ————	<i>Trioracodon</i>	
	<i>Priacodon</i>	<i>Triconodon</i>	
	<i>Tinodon</i>	<i>Spalacotherium</i> <i>Peralestes</i>	
	<i>Amphidon</i> <i>Eurylambda</i>		
	<i>Paurodon</i> <i>Archaeotrigon</i> <i>Tathiodon</i>	<i>Peramus</i>	<i>Brancatherulum</i>
	<i>Dryolestes</i> <i>Laolestes</i> <i>Amblotherium</i> ————	<i>Amblotherium</i>	
	<i>Kepolestes</i>	<i>Peraspalax</i> <i>Phascolestes</i>	
	<i>Herpetairus</i> <i>Melanodon</i> <i>Euthlastus</i> <i>Miccylyotyrans</i> <i>Malthacolestes</i> <i>Pelicipsis</i>	<i>Kurtodon</i>	
	<i>Docodon</i>	<i>Peraiocynodon</i>	

MIDDLE  
JURASSIC*Stereognathus**Amphilestes**Phascolotherium**Amphitherium*

## RHAETIC

*Tritylodon* ——— *Tritylodon**Oligokyphus**Chalepotherium**Archaeodon**Microcleptes**Thomasia**Hypsiprymnopsis*

The Morrison of North America and the Purbeck of England are almost or quite contemporaneous. The Amphidontidae are as yet unrepresented in the Purbeck, but members of this family are excessively rare in the Morrison and their apparent absence in England is no doubt due to lack of discovery. Aside from this, all the known families are common to the two faunas and are in about the same stage of evolution in each. *Ctenacodon* among the multituberculates, *Trioracodon* among the triconodonts, and *Amblotherium* among the pantotheres occur in both, and the other genera, while quite distinct, are for the most part closely comparable. The correspondence between the two faunas is sufficiently close to warrant the following three conclusions:

1. The Purbeck and the Morrison mammalian faunas are of similar facies.
2. They are of nearly or quite the same age.
3. They were apparently derived from a common center and indicate that an avenue of migration practicable for small mammals linked England and western North America some time in the Upper Jurassic, either directly or through this common center.

The differences are all explicable on the basis of wide geographic separation, in view of the presumably feeble migratory powers of the mammals, without postulating any definite intervening barrier or any marked difference in facies.

## SUCCESSION OF EARLY MAMMALIAN FAUNAS

The known distribution in time and succession of the Mesozoic orders and families is shown in the following table:



	<i>Upper Triassic</i>	<i>Middle Jurassic</i>	<i>Upper Jurassic</i>	<i>Upper Cretaceous</i>	<i>Tertiary</i>
Multituberculata	x ————— x	x	x	x	x
Tritylodontidae	x ————— x				
Microcleptidae	x				
Plagiaulacidae			x		
Ptilodontidae				x ————— x	
Taeniolabididae					x
Triconodonta		x ————— x			
Triconodontidae		x ————— x			
Symmetrodonta			x		
Spalacotheriidae			x		
Amphidontidae			x		
Pantotheria		x ————— x			
Amphitheriidae		x			
Paurodontidae			x		
Dryolestidae			x		
Docodontidae			x		
Marsupialia				x ————— x	
Didelphiidae				x ————— x	
Insectivora				x ————— x	
Zalambdalestidae				x ————— ?	
Leptictidae				x ————— x	
Deltatheridiidae				x ————— x	

At first glance several broad facts regarding the known succession are notable. The poorly known upper Triassic fauna does not contain the ancestors of any later mammals with the possible exception of the single genus *Stereognathus* of the middle Jurassic. The middle and upper Jurassic faunas of England are, to be sure, rather different but there is reason to believe that they were essentially continuous and that the differences are largely due to the considerable lapse of time and to the imperfection of our knowledge. The break between the upper Jurassic and the upper Cretaceous is vast. Except for the transitional steps between reptiles and mammals, this is far the greatest remaining gap in the knowledge of mammalian history. The break between the upper Cretaceous and the Paleocene is slight from an evolutionary point of view, the known Cretaceous groups mostly continuing with but slight advances in structure, but it is strongly marked in the known areas by the introduction from some unknown source of numerous new mammalian groups, not shown in the table.

Further discussion of the Triassic fauna and of its relationships to the successive waves of expansion within the order would be futile. It may represent a primary spreading of non-ancestral groups from the center of mammalian origin, but it is so poorly known that it offers no valid grounds for conclusions, either positive or negative, save that mammals of a sort were then in existence but that the known forms have no significance with regard to the origin of later mammals.

The resemblance of the Stonesfield and Purbeck faunas in England is such as to warrant the tentative conclusion that there were no changes of prime importance in the distribution of the larger mammalian groups in this area during the middle and upper Jurassic. They apparently belong to the same distributional wave or radiation. The faunal relationships between the upper Jurassic and upper Cretaceous faunas and between the latter and the Paleocene faunas demand closer analysis.

Marsh was the first to treat this question. He believed (1892A, pp. 250-1) that the mammals of the Lance "are not transitional between Mesozoic and Tertiary forms, but their affinities are with the former beyond a doubt. . . . The . . . Puerco is clearly Tertiary, and the great break is between this horizon and the Ceratops beds of the Laramie. . . . Instead of placing them close together, as some geologists seem inclined to do, it will be more profitable in future to search for the great series of intervening strata containing the forms that lead from one to the other. . . . Bearing in mind all that is known to-day [1892] of the development and succession of Vertebrate life in America, from the early Silurian on to the present time, it is safe to say that the faunal break as now known between the Laramie and the lower Wahsatch [Puerco] is far more profound than would be the case if the entire Jurassic and the Cretaceous below the Laramie were wanting. . . ." The essential elements of this view are (1) belief in the close relationship of the Lance fauna to that of the Morrison, (2) recognition of the great difference between the known Lance and Puerco faunas, and (3) the assumption that this difference is due not to migrations or changes of facies but to evolution in place during a long period unknown by mammalian fossils.

This view of Marsh was strongly combated by Osborn who disagreed with Marsh on every point. In 1893 Osborn stated that, "The fact is, these Laramie mammals are surprisingly near those of the Puerco, and in some cases almost identical with them; in other cases they are of a somewhat older type. Therefore, *the greatest gap to be filled by future discovery is between this Laramie fauna and the Jurassic*.<sup>1</sup> For this Laramie fauna is separated from the Puerco about as widely as the Puerco is from the Wahsatch, but no more widely; whereas it is separated by a profound gap from the Jurassic fauna . . . [The Lance *Cimolomys* (referred to *Ptilodus* by Osborn) and the Torrejon (upper Puerco of Cope and Osborn) *Ptilodus*] are in substantially the same stage of dental evolution, and so nearly alike that the writer was for a long time tempted to believe that the Laramie and Puerco faunae were contemporaneous. . . . Two features make the Laramie ["trituberculate"] fauna appear more ancient than the Puerco: first, the non-development of an internal cingulum, which is common in the Puerco; second, the entire absence of the hypocone, which is quite strong in some Puerco mammals. On the other hand [certain of the] upper and lower molars . . . are analogous to *Ectoconus*, *Dissacus*, *Diacodon*, and *Haploconus* of the Puerco [or Torrejon]."

Thus Osborn's chief conclusions were (1) that there is a profound gap between the Lance and the Morrison, (2) that the Lance and Puerco faunas are closely related and in a comparable stage of evolution so that they were close to each other in time, or

<sup>1</sup> Italics Osborn's.



even contemporaneous, and (3) that the imperfectly known Lance fauna may have included the immediate ancestors of the Puerco fauna so that it may be that there is no important distinction between them due either to facies or to immigration of new forms and extinction of old.

Some minor points have since been altered by Osborn, such as his more definite recognition that many of the Puerco mammals have no apparent Cretaceous ancestry and are of unknown origin, but his later generalizations have been chiefly based on these views. In his most important study devoted specifically to the problems here under consideration (1905) Osborn advanced the view that there had been four great mammalian radiations: (1) a Jurassic radiation of doubtful relationships to the later mammals, (2) a Cretaceous and Tertiary radiation of Marsupialia, chiefly in Australia, Antarctica (hypothetical), and South America, (3) a Cretaceous and lower Tertiary radiation of archaic, chiefly non-ancestral placentals, and (4) a Tertiary radiation of higher or modernized placentals. The members of the third radiation he had previously called the Meseutheria or archaic placentals, those of the fourth radiation the Ceneutheria or modernized placentals.

The view, first advanced by Osborn, that there is a vast break between the Jurassic faunas of Europe and America and the known upper Cretaceous faunas has not been seriously questioned and is on an even stronger basis today than when first proposed. The Jurassic triconodonts and symmetrodonts disappeared without issue in the course of lower Cretaceous time or at the beginning of the Cretaceous. The multituberculates continued, but with modifications rather more important than was realized twenty or thirty years ago. These modifications may have been due entirely to evolution more or less in place during the long gap in our knowledge, but it is somewhat more probable that the origin of the Cretaceous and Paleocene multituberculates is to be sought in some post-Jurassic center of radiation and that they are immigrants where found. Marsupials and placentals apparently are not present as such in the Jurassic faunas and here, too, it is probable that they originated from a Jurassic group (the Pantotheria in a broad sense) in some definite center of evolution and hence spread throughout the world in the Cretaceous. Recognizing the essentially tentative and inaccurate nature inherent in the broadest generalizations, it is nevertheless useful and permissible to consider, as did Osborn, that the Jurassic and Cretaceous mammalian faunas as known represent two great separate mammalian radiations.

The known members of the Cretaceous radiation belonged to only three orders: Multituberculata, Marsupialia, and Insectivora. This involved the original radiation of the Marsupialia and the present writer cannot follow Osborn's older view that the marsupial radiation was separate from that of the placentals primarily. They spread over the world in company with the other Cretaceous mammals. Their later radiations in South America and in Australia are of secondary scope, not on the same plane as the three or four great primary mammalian radiations here discussed. The whole problem is greatly complicated by the fact that secondary radiations of this sort, confined to single land masses, and still more limited local radiations were of constant occurrence, along with intermittent migrations between the various continental and local



centers. But these complications do not vitiate the general idea of primary mammalian radiations which we owe to Osborn and which is such a helpful concept in considering the course of mammalian history as a whole.

Because of these intricate lesser factors and the general inadequacy of the present data, the problem of the relationship between Cretaceous and Paleocene mammals is the most difficult of all from a faunal point of view. Marsh's belief in a great time gap between the Lance and the Puerco must be abandoned. Increasing stratigraphic knowledge makes it more and more apparent that there is, geologically speaking, no considerable time interval in the Late Cretaceous and Paleocene unrepresented by sediments in the North American West. It is also clear, on stratigraphic grounds alone, that the Lance and Puerco were very close to one another in time. This is strongly supported by the mammalian evidence as now interpreted. The representatives in the Paleocene of the Multituberculata, Marsupialia, and Insectivora are hardly appreciably advanced over their Lance forerunners. A new and rather distinctive group of multituberculates, the Taeniolabididae, appears, and the marsupials become much less numerous and less varied. The former fact is due to immigration or change of facies or both, the latter to extinction or change of facies or, most likely, both.

As is now universally recognized, the essential difference between the Lance and Paleocene faunas lies in the presence in the latter of very numerous new groups. This difference is very marked, the new groups comprising almost the entire later fauna. There are three possible explanations: (1) that the apparently new mammals are the result of evolution from the known Lance forms or their close allies, (2) that their ancestors were actually present here in Lance time but are unknown because they were of a very different facies from that of any late Cretaceous deposit, or (3) that the majority of the Paleocene mammals originated elsewhere than in the known fossiliferous areas and appeared suddenly by migration from some unknown center consequent with some geographic change permitting their spread. The first explanation must be abandoned in view of the now reasonably certain knowledge of the true affinities of the Lance mammals and of the extreme shortness of the time which could be allotted for their further evolution before the Paleocene.

The second view, that the Lance and Puerco differ sharply in facies but little if any in age and that the Paleocene mammals were already present in the known Paleocene areas in the Cretaceous, seems to be inevitably involved in Osborn's view of a mesoplacentalian, Cretaceous-Lower Tertiary radiation. It is also the most essential feature in Matthew's explanations of this break in faunas. This authority states (1928, p. 953) that "the Paleocene mammals belong to Cretaceous orders. It is essentially the culmination of a Cretaceous mammal fauna, although living in the beginning of the Tertiary period as the lines are usually drawn." Such an expression might mean only that the Paleocene orders had Cretaceous ancestors and were already differentiated in the Cretaceous; but all mammals naturally had Cretaceous ancestors, and it is highly probable that the Eocene orders also were already differentiated in the latest Cretaceous. Every mammal fauna is the continuation, if not necessarily the culmination, of some fauna of the preceding period or epoch. What must be, and from Dr. Mat-

thew's other writings apparently is, meant is that the spread of the Paleocene orders took place in the Cretaceous, that the Paleocene distribution is the result of a Cretaceous radiation. As Matthew has explicitly recognized, this necessarily involves a belief that the Lance and Paleocene faunas differ chiefly in facies.

The evidence is indirect or negative, and consequently hard to disprove, but in the present writer's opinion this view does not square well with the known facts. Some difference in facies there may be, but the more remarkable faunal differences probably cannot be explained on this basis. The uppermost Cretaceous and Paleocene continental sediments suggest no definite difference in facies. The floras are almost identical. Animals of such limited facies as the champsosaurs occur with both types of mammalian faunas, and the Cretaceous mammals themselves all have close ecological analogues in the Paleocene faunas. Yet on the one hand are three mammalian families associated with abundant and varied dinosaurs, on the other no trace of dinosaurs and the same three mammalian families along with some ten other families unknown in any previous fauna. Such differences are quite unknown among different facies of land faunas in the same region at any other time in the history of vertebrates. Ignorance of the Lance fauna cannot be urged as a complete explanation. The remains are so fragmentary as to be dubious in many respects, but they clearly are not ancestral to the great majority of Paleocene mammals, many individual specimens are known—several hundreds—and the fauna is known to have been essentially the same in Lance time over a large area, for specimens from Montana, South Dakota, and Wyoming are known. Furthermore the earlier Belly River has yielded a few remains which indicate that its mammalian fauna was of this same type.

Without ignoring the alternative hypothesis, it seems more reasonable (1) that there was a Cretaceous type of mammalian fauna in the American West just as there was a Paleocene type and an Eocene type regardless of strictly evolutionary changes, (2) that the Paleocene fauna was *not* the culmination of any previous fauna in the same region, but (3) that the beginning of the Paleocene was here marked by migratory movements of the first magnitude involving the introduction of new groups which had been evolving in some unknown center while the multituberculate-marsupial-insectivore fauna, resultant of an earlier radiation, was dominant.

## RÉSUMÉ OF FAUNAL SUCCESSION

So far as can now be judged from the evidence of the known early mammals, the following may have been the major events in mammalian history:

1. The origin of true mammals from the cynodont reptiles or closely related forms, probably in the Triassic. This may have been followed by a sort of proto-mammalian Rhaetic radiation of the tritylodontids, microcleptids, and possibly some other groups.
2. A Jurassic radiation, world-wide in scope, involving the Multituberculata, Triconodonta, Symmetrodonta, and Pantotheria.



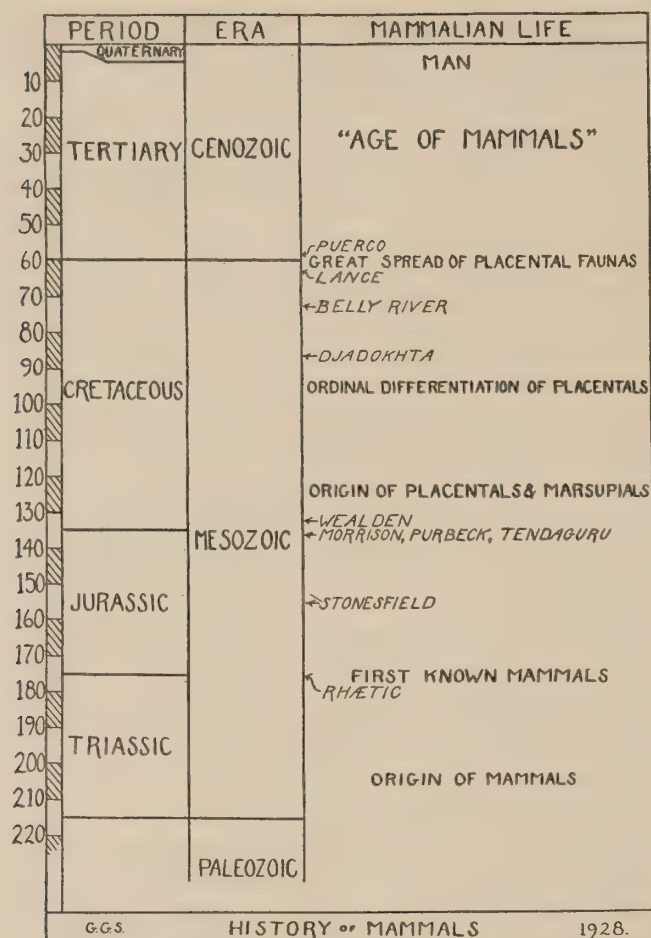


FIG. 62. Diagram showing the relative positions in time of the known Mesozoic mammalian faunas and the approximate relative dates of some of the major events in mammalian history. The figures on the left represent millions of years and are essentially those advanced by Professor Arthur Holmes (*The Age of the Earth*, London, 1927) on a correlation of radioactive and other data. The relative duration of the periods is fairly well established, the absolute chronology still open to question.

by the Cretaceous radiation, or part of it, but by no subsequent radiation, except accidentally, until recent time. South America apparently lost connection with the rest of the world after the Paleocene radiation had reached it and was not reunited until late Miocene or Pliocene time.

3. A Cretaceous radiation, from some center reached by at least the Multituberculata and Pantotheria of the previous radiation, involving more advanced members of the Multituberculata, and, for the first time, marsupials and placentals, probably derived from the Pantotheria.

4. A Paleocene radiation, from some center reached by the Insectivora, involving the archaic placentals, Meseutheria of Osborn.

5. An Eocene radiation, possibly from the same center as that of the Paleocene radiation, involving the modernized mammals, Ceneutheria of Osborn, of ultimate common derivation with the archaic mammals.

Each of these five events probably had a definite focus or center, and the five centers probably did not all coincide. Nothing is yet certainly known as to the location of any one of them.

Secondary radiations, intermigrations, local or widespread extinctions, and so forth, were of constant occurrence.

Australia was probably reached



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# GENERIC INDEX

THE following list includes the names which have been used for genera of American Mesozoic mammals, with the page on which their principal treatment begins in this memoir. Genera not now considered valid in this sense, whether through synonymy, homonymy, or incorrect reference, are in italics.

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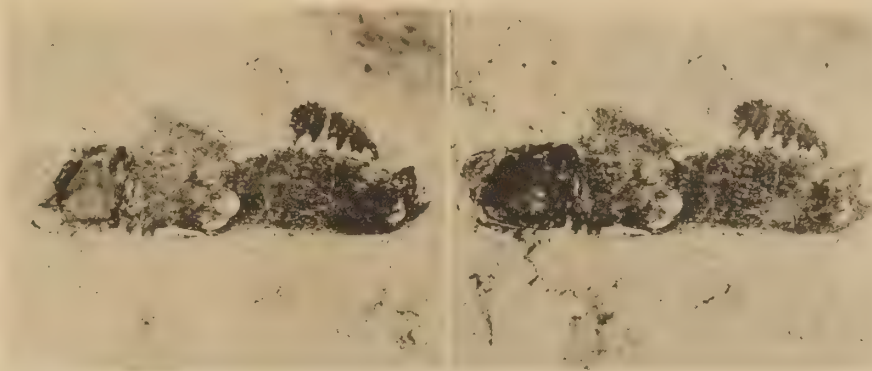
## PLATES



## PLATE I

	Described on Page
<i>Ctenacodon serratus</i> Marsh.	16
FIG. 1. Left lower jaw with P <sub>1-4</sub> , internal view. X 3 diam. Y.P.M. No. 13668.	
<i>Ctenacodon scindens</i> Simpson.	20
FIG. 2. Part of right lower jaw with P <sub>3-4</sub> and M <sub>1-2</sub> , external view. X 9 diam. Type. Y.P.M. No. 10366.	
<i>Ctenacodon</i> sp.	18
FIG. 3. M <sub>1</sub> , crown view. X about 25 diam. Y.P.M. No. 13666.	

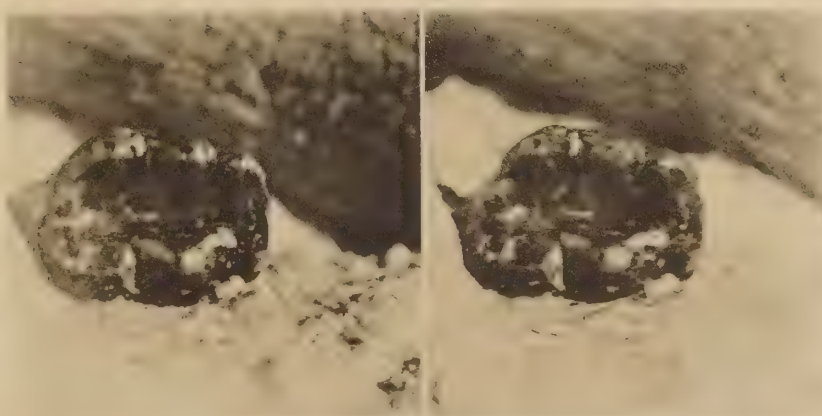
Plates I-XXI consist of stereoscopic microphotographs, enlarged from two to twenty-five diameters. They should be viewed either with a stereoscope designed to be placed on a horizontal page or with a stereoscope of the more usual pattern with the projecting arm (designed to carry the postcard-sized stereographs) cut off at two or three inches from the prisms.



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## PLATE II

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### *Ctenacodon serratus* Marsh.

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FIG. 1. Right lower jaw with  $P_{1-4}$  and  $M_1$ , crown view. X 6 diam. Type.  
Y.P.M. No. 11833.

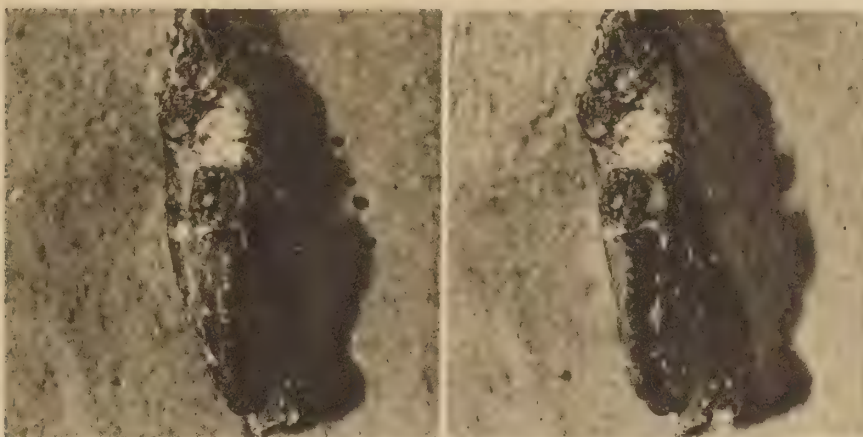
FIG. 2. Left lower jaw with  $P_{1-4}$  and  $M_{1-2}$ , external view. X 9 diam.  
(Type of *Ctenacodon nanus*.) Y.P.M. No. 11832.

### *Ctenacodon laticeps* (Marsh).

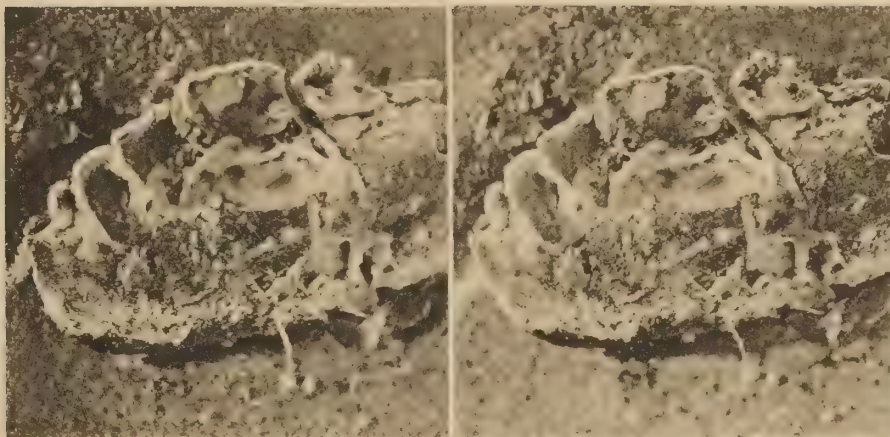
21

FIG. 3. Left upper jaw with  $P^{1-5}$  and  $M^{1-2}$ , crown view. X 7 diam. Type.  
Y.P.M. No. 11761.

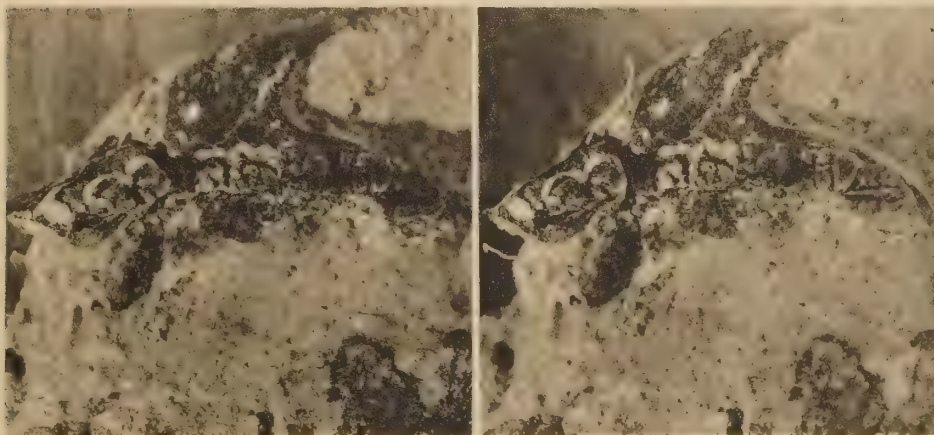




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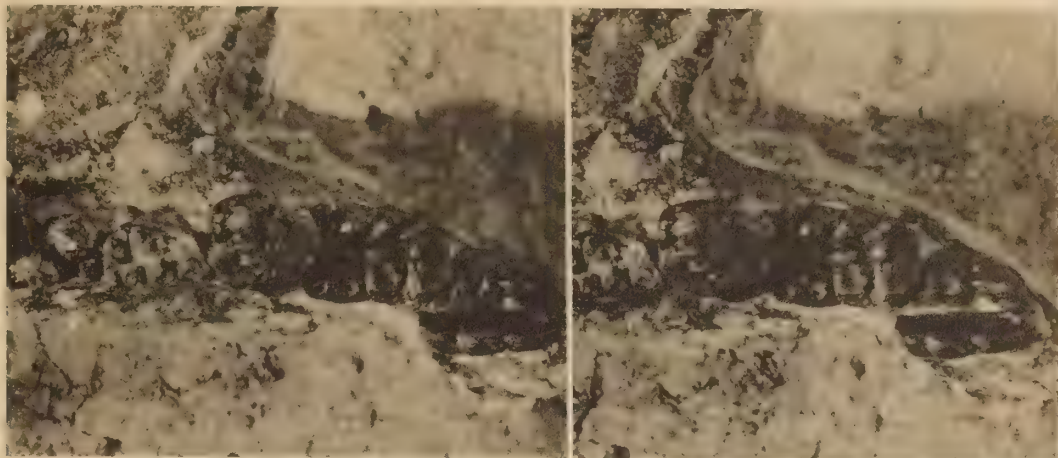
### PLATE III

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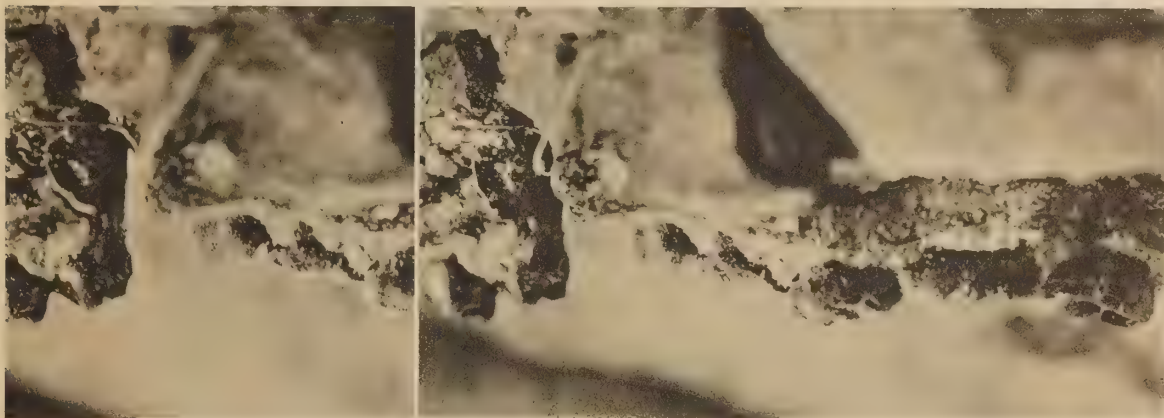
*Ctenacodon laticeps* (Marsh).

21

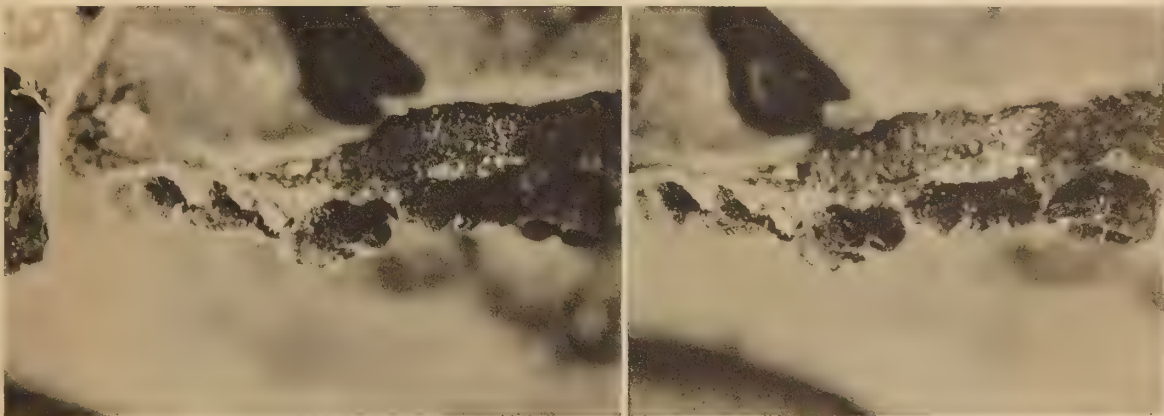
- FIG. 1. Detail of same specimen as Pl. II, fig. 3, crown view. Stereoscopic: P<sup>5</sup>-M<sup>2</sup>, part of P<sup>4</sup>. Not stereoscopic (left figure): P<sup>3</sup>, anterior part of P<sup>4</sup>. X 15 diam. Type. Y.P.M. No. 11761.
- FIG. 2. Same specimen, external view. Stereoscopic: P<sup>1-4</sup>, part of P<sup>5</sup>. Not stereoscopic (right figure): part of P<sup>5</sup>, M<sup>1-2</sup>. X 15 diam.
- FIG. 3. Same specimen, external view. Stereoscopic: P<sup>3</sup>-M<sup>2</sup>. Not stereoscopic (left figure): P<sup>2</sup>. X 15 diam.



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## PLATE IV

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*?Psalodon marshi* Simpson.

27

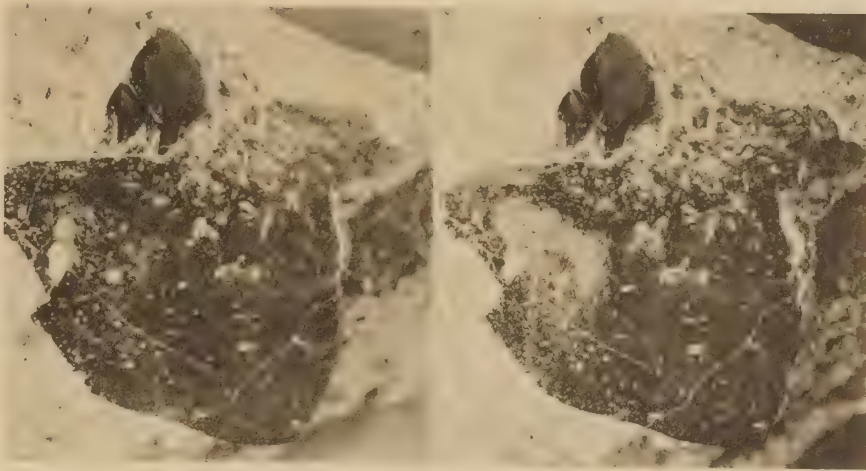
FIG. 1. Left lower jaw with  $P_{1-2}$ , external view. X 6 diam. Y.P.M. No. 13672.

FIG. 2. Isolated right  $P_4$ , external view. X 14 diam. Y.P.M. No. 13669.

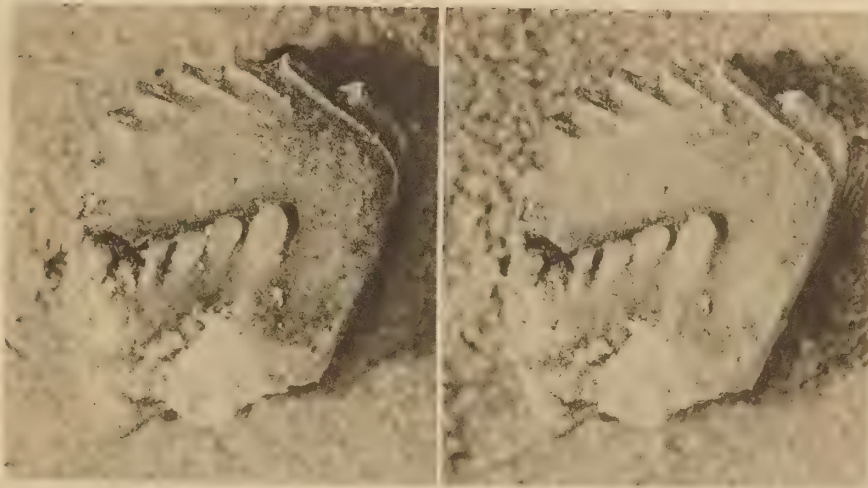
*Psalodon potens* (Marsh).

26

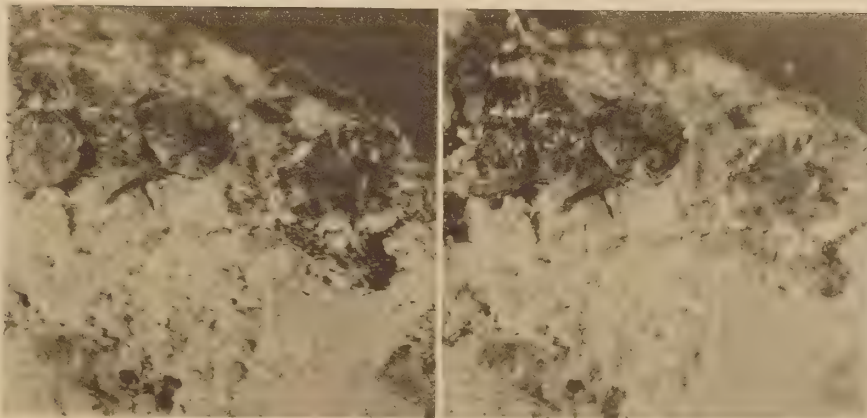
FIG. 3. Right upper jaw with  $P^1$  and  $P^{3-4}$ , crown view. X 8 diam. Y.P.M. No. 10363.



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## PLATE V

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### *Psalodon potens* (Marsh).

26

FIG. 1. Right upper jaw with P<sup>3-5</sup>, external view. X 8 diam. Type. Y.P.M.  
No. 11834.

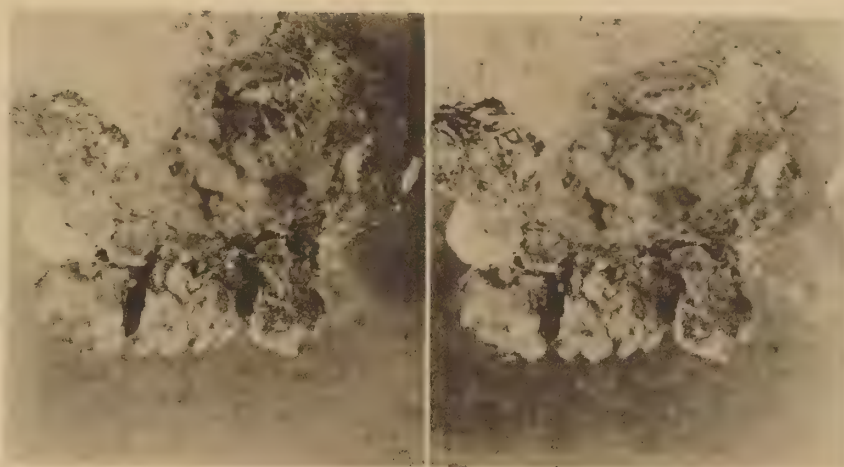
FIG. 2. Same specimen, crown view. X 10 diam.

### *Psalodon fortis* (Marsh).

26

FIG. 3. Right premaxilla with I<sup>2-3</sup>, internal view. X 8 diam. Type.  
Y.P.M. No. 11760.

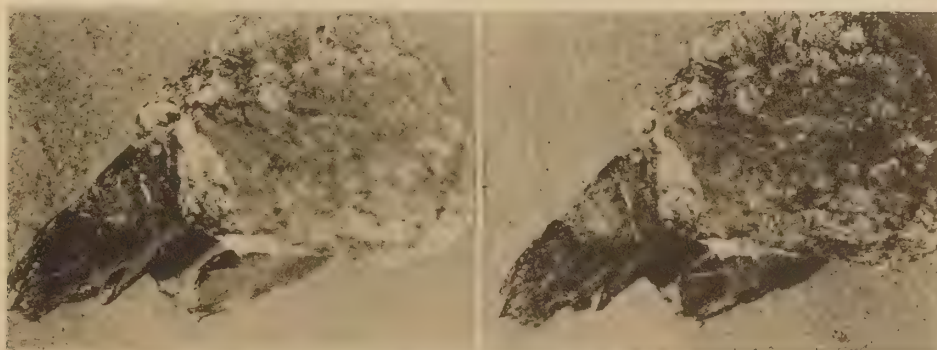




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PLATE VI

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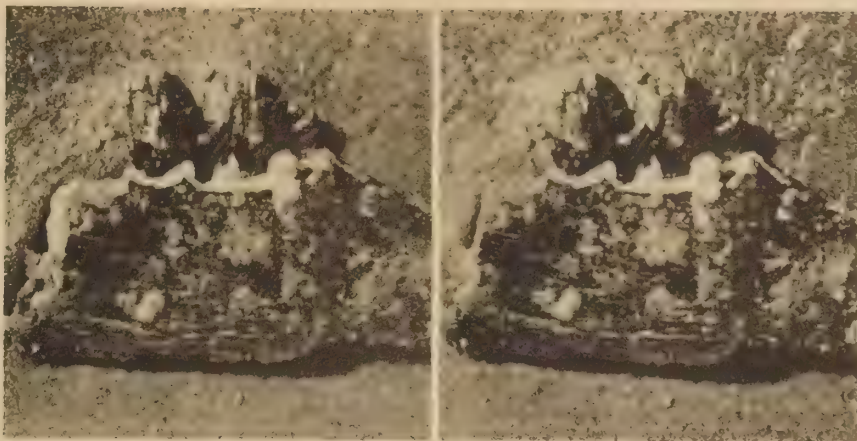
*Tathiodon agilis* Simpson.

53

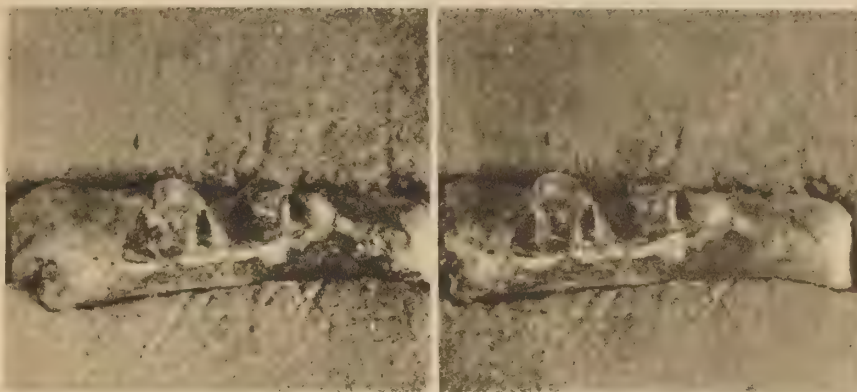
FIG. 1. Left lower jaw with two molars, internal view. X 10 diam. Type.  
Y.P.M. No. 13649.

FIG. 2. Same specimen, crown view. X 10 diam.

FIG. 3. Same specimen, internal view. X 10 diam.



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## PLATE VII

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*Archaeotrigon distagmus* Simpson.

52

FIG. 1. Right lower jaw with  $M_{2-3}$ , crown view. X 15 diam. Type. Y.P.M. No. 13641.

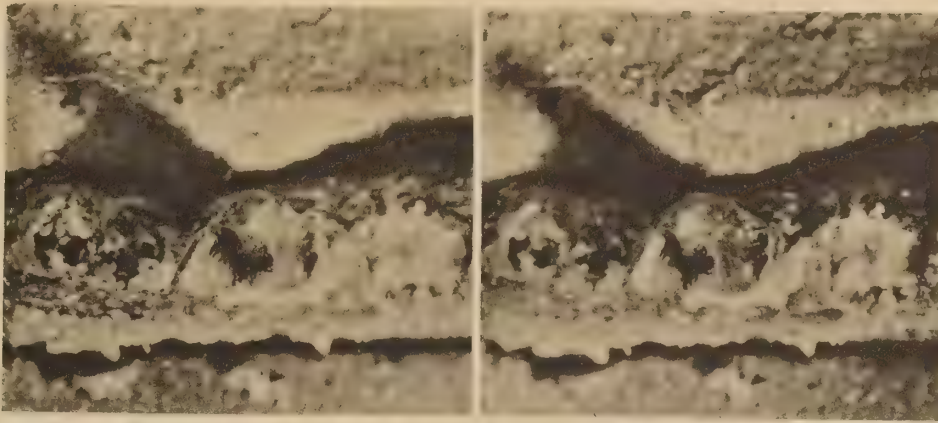
*Archaeotrigon* sp.

FIG. 2. Isolated right lower molar, internal view. X about 20 diam. Y.P.M. No. 13640.

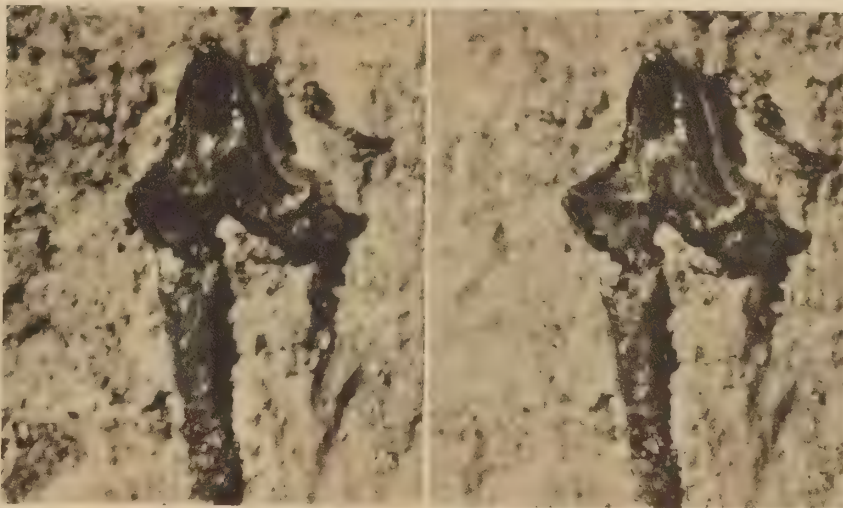
*Dryolestes priscus* Marsh.

58

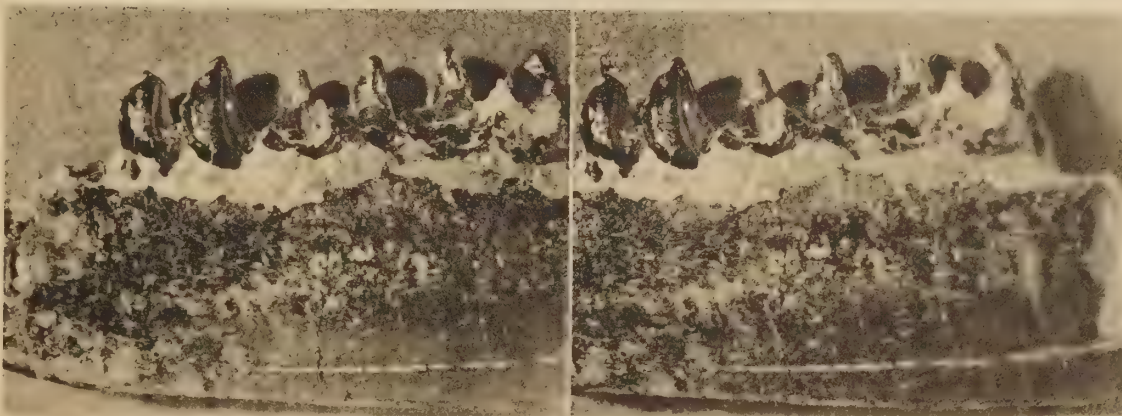
FIG. 3. Right lower jaw with  $P_{3-4}$  and  $M_{1-4}$ , internal view. X 9 diam. Parts of jaw with teeth missing are not stereoscopic. (Type of *Stylacodon validus*.) Y.P.M. No. 11884.



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PLATE VII—ARCHAEOTRIGON, DRYOLESTES

## PLATE VIII

Described  
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### *Dryolestes priscus* Marsh.

58

FIG. 1. Right lower jaw with  $P_{1-4}$  and  $M_{1-4}$ , external view. Stereoscopic:  $P_{1-4}$ ,  $M_1$ , and part of  $M_2$ . Not stereoscopic (left figure): part of  $M_2$ ,  $M_{3-4}$ . X 9 diam. (Type of *Asthenodon segnis*.) Y.P.M. No. 10646.

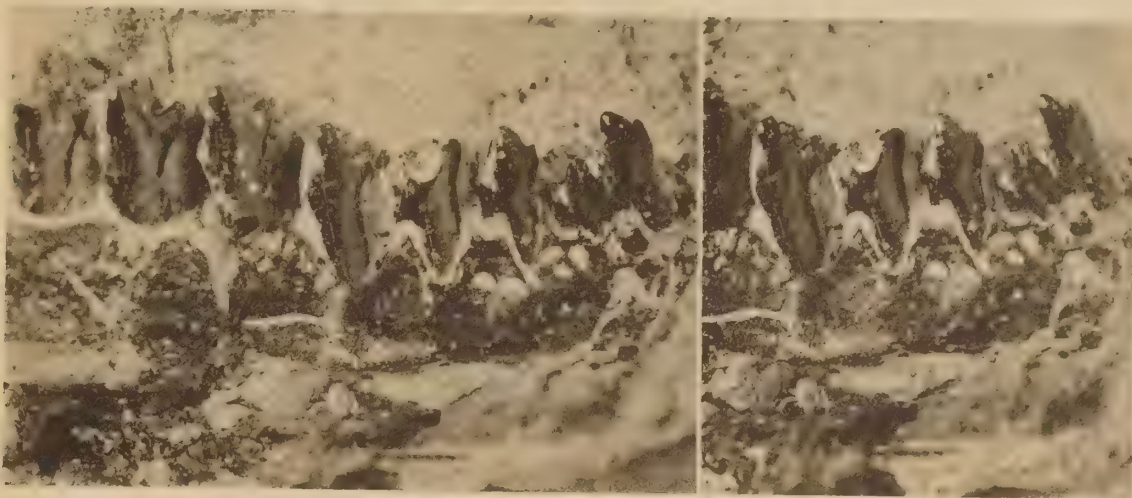
### *Laolestes eminens* Simpson.

61

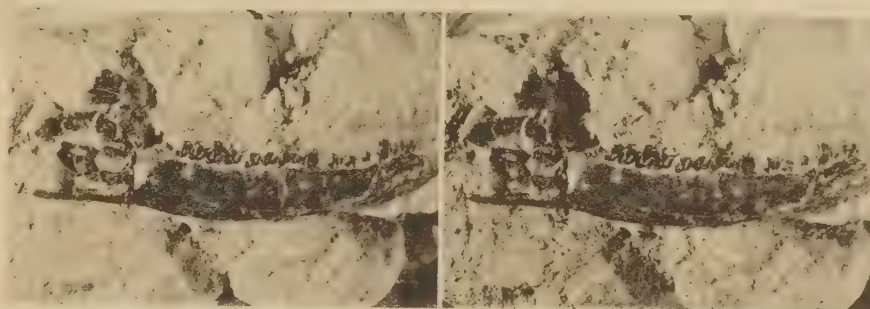
FIG. 2. Left lower jaw with  $I_{3-4}$ , C,  $P_{1-3}$ , and  $M_{1-8}$ , internal view. X 2 diam. Type. Y.P.M. No. 13719.

FIG. 3. Right lower jaw with  $P_{3-4}$  and  $M_1$ , internal view. More anterior and posterior parts not stereoscopic. X 10 diam. Y.P.M. No. 13725.





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## PLATE IX

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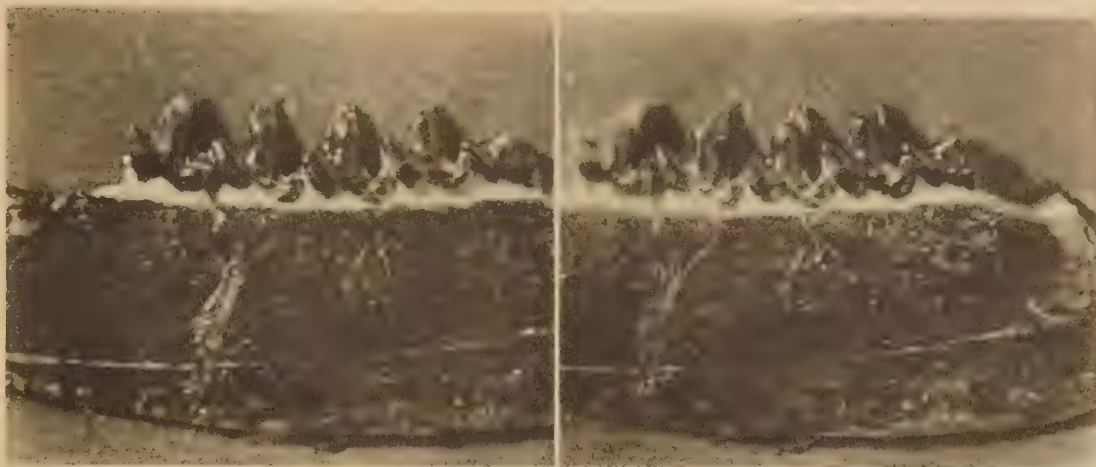
### *Laolestes eminens* Simpson.

61

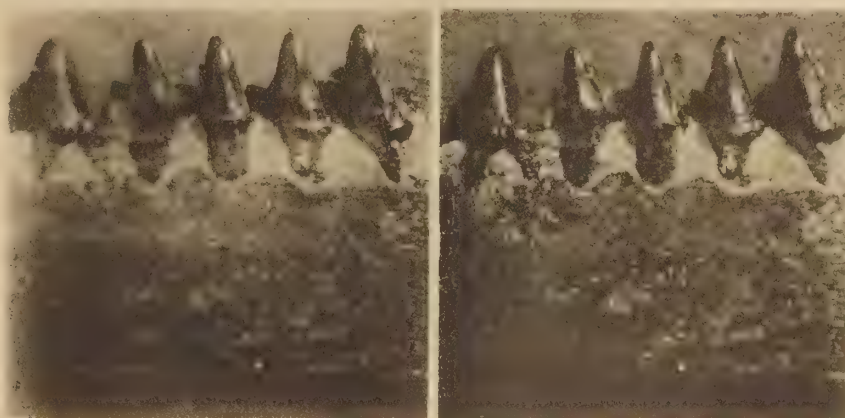
FIG. 1. Right lower jaw with  $M_{3-7}$ , internal view. More anterior and posterior parts not stereoscopic. X 10 diam. Y.P.M. No. 13720.

FIG. 2. Left lower jaw with  $P_4$  and  $M_{1-4}$ , external view. X 10 diam. Y.P.M. No. 10662.

FIG. 3. Same specimen, internal view. X 10 diam.



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## PLATE X

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### *Laolestes eminens* Simpson.

61

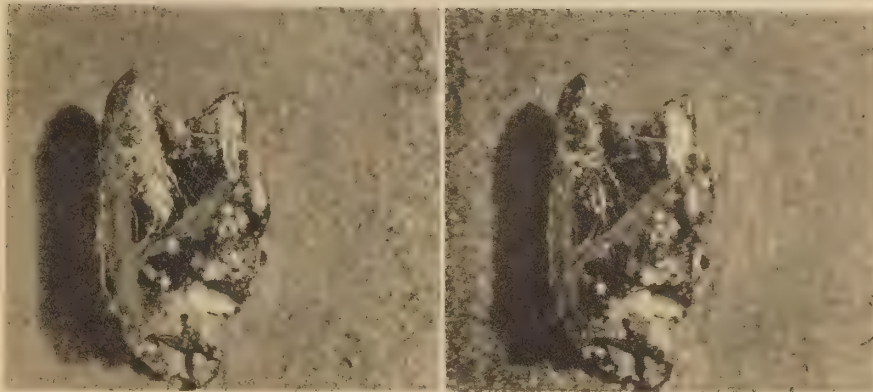
FIG. 1. Same specimen as Pl. IX, figs. 2-3. Left lower jaw with  $P_4$  and  $M_{1-4}$ , crown view. X 10 diam. Y.P.M. No. 10662.

FIG. 2. Isolated left lower molar, posterior view. X 20 diam. Y.P.M. No. 13726.

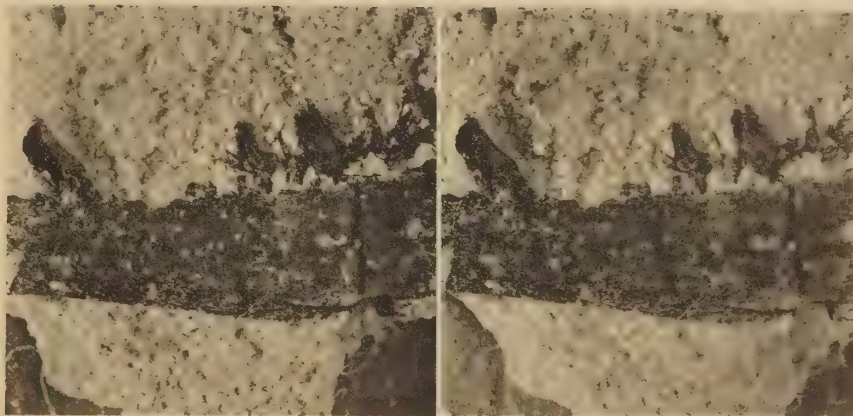
FIG. 3. Right lower jaw with C,  $P_{3-4}$ , and  $M_{1-2}$ . X 6 diam. Y.P.M. No. 10661.



I



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## PLATE XI

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### *Laolestes grandis* Simpson.

64

FIG. 1. Right lower jaw with  $M_{1-4}$ , crown view. X 9 diam. Type. Y.P.M. No. 13727.

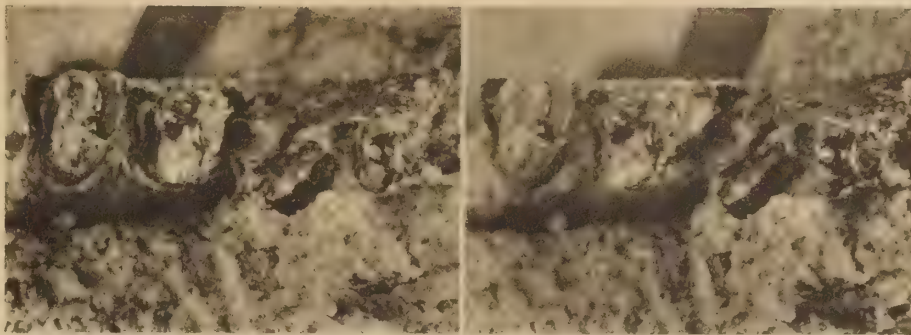
### *Amblotherium gracilis* (Marsh).

66

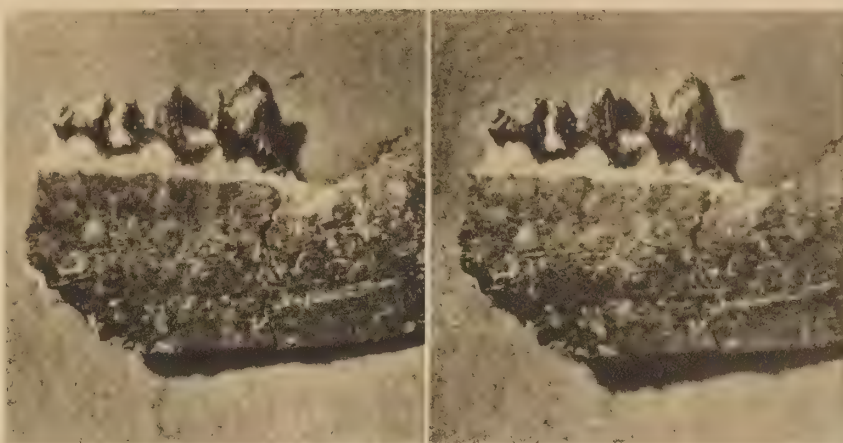
FIG. 2. Right lower jaw with  $M_{5-7}$ , internal view. X 12 diam. Y.P.M. No. 13732.

FIG. 3. Left lower jaw with  $P_4$  and  $M_{1-4}$ , external view, and  $P_3$  (detached, on matrix anterior to  $P_4$ ), internal view. X 12 diam. Type. Y.P.M. No. 11883.

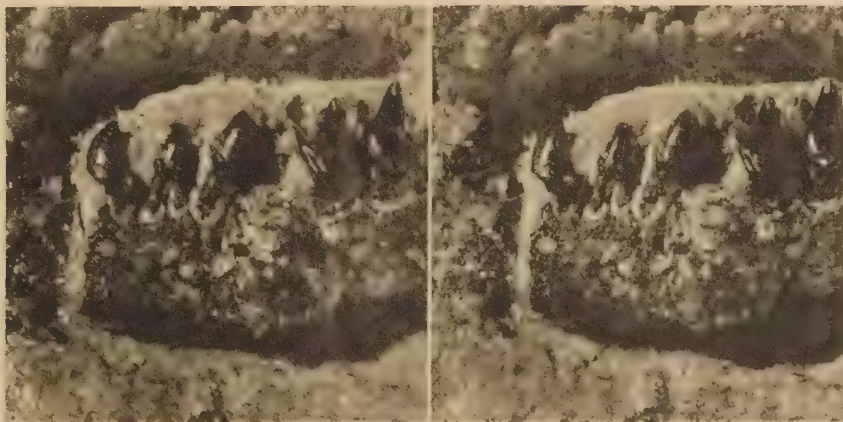




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## PLATE XII

### *Amblotherium debilis* Simpson.

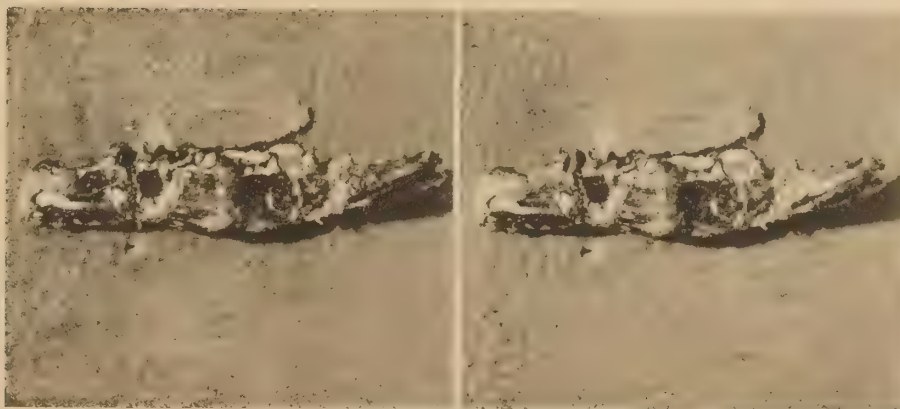
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68

FIG. 1. Left lower jaw with  $M_{1-6}$ , poorly preserved, internal view. X 6 diam. Type. Y.P.M. No. 11821.

FIG. 2. Right lower jaw with  $M_{1-6}$ , external view. Posterior part (left figure) not stereoscopic. X 9 diam. Y.P.M. No. 13728.

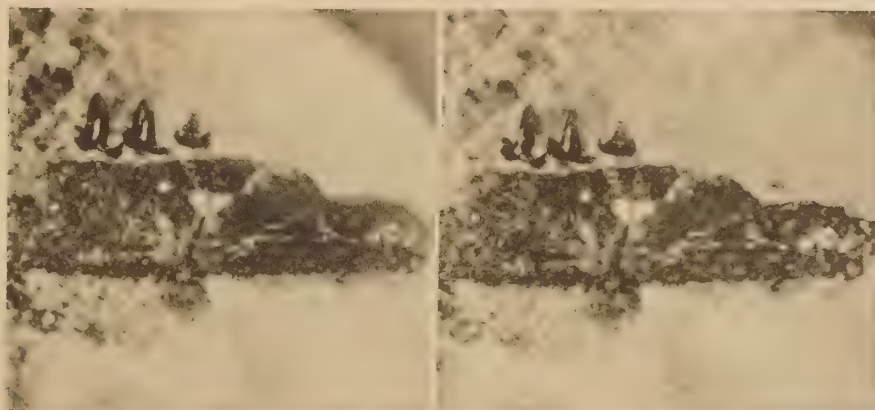
FIG. 3. Right lower jaw with  $M_{5-7}$ , internal view. X 9 diam. Y.P.M. No. 13730.



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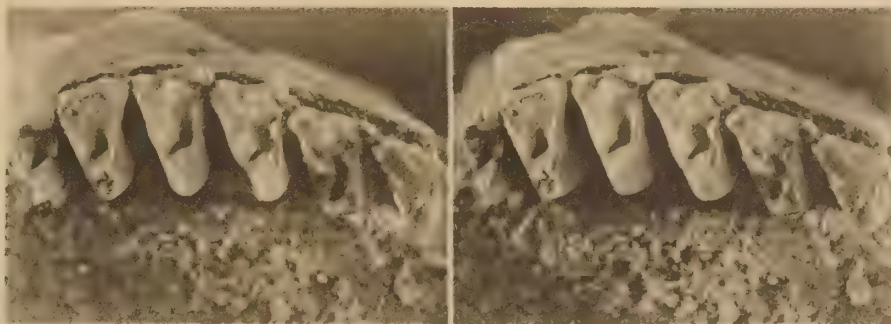


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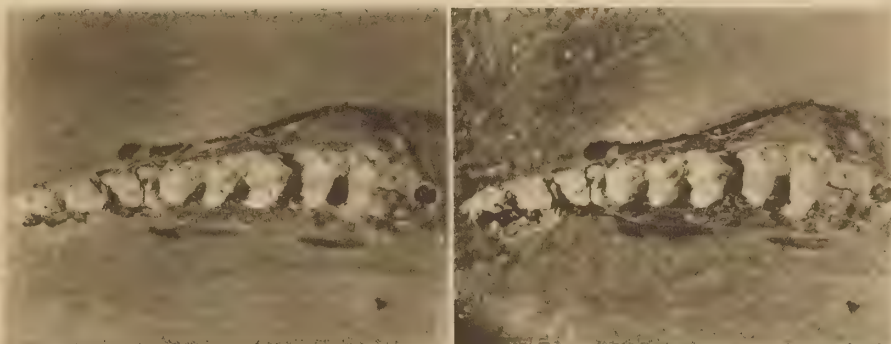


## PLATE XIII

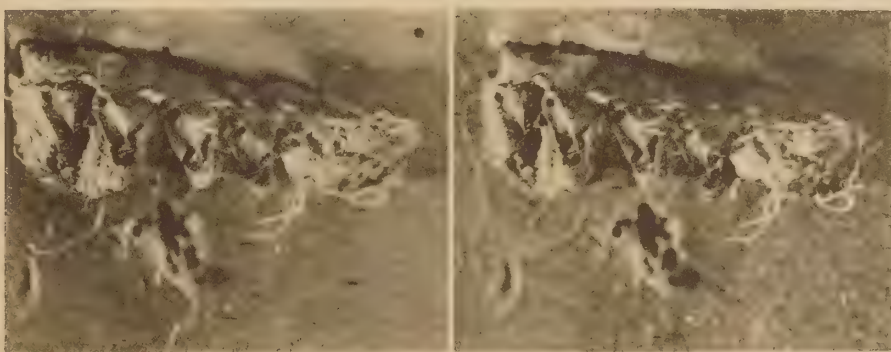
	Described on Page
<i>Herpetairus arcuatus</i> (Marsh).	72
FIG. 1. Right upper jaw with M <sup>2-7</sup> , crown view. X 9 diam. Type. Y.P.M. No. 11822.	
<i>Herpetairus</i> or <i>Melanodon</i> sp.	77
FIG. 2. Left upper jaw with P <sup>3</sup> and M <sup>1-5</sup> , crown view. X about 6 diam. (Type of <i>Dryolestes obtusus</i> .) Y.P.M. No. 11819A.	
<i>Melanodon oweni</i> Simpson.	75
FIG. 3. Right upper jaw with P <sup>4</sup> and M <sup>1-5</sup> , crown view. X 6 diam. Type. Y.P.M. No. 10663.	



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## PLATE XIV

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*Melanodon oweni* Simpson.

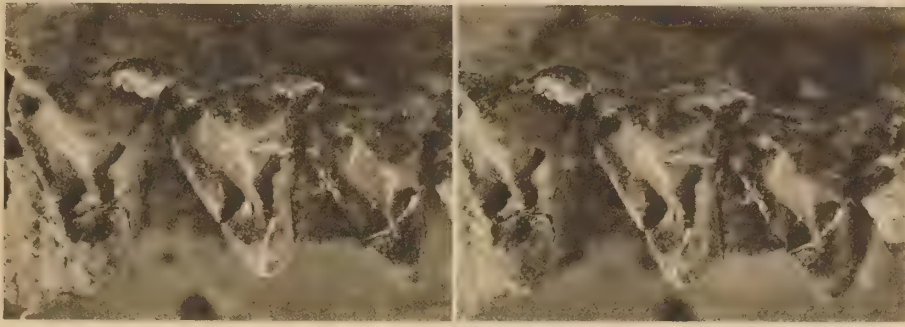
75

FIG. 1. Same specimen as Pl. XIII, fig. 3. Detail showing right  $M^{2-4}$ , crown view. X 13 diam. Type. Y.P.M. No. 10663.

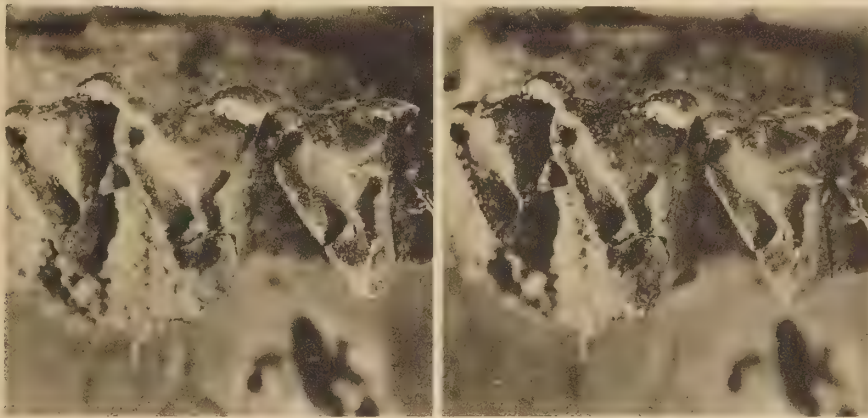
FIG. 2. Same specimen. Detail showing right  $M^{3-5}$ , crown view. X 13 diam.

FIG. 3. Same specimen. Right upper jaw with  $P^4$  and  $M^{1-5}$ , external view. X 5 diam.

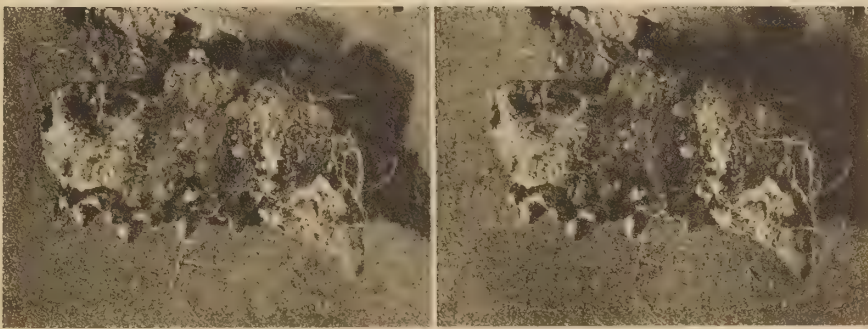




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PLATE XV

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*Melanodon goodrichi* Simpson.

76

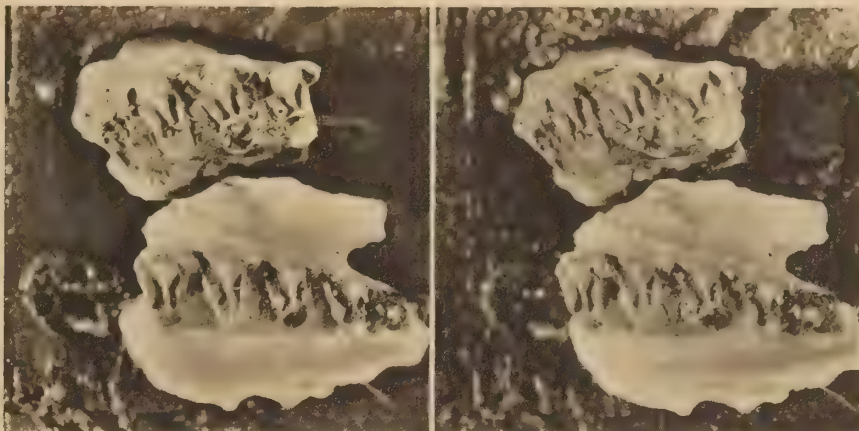
FIG. 1. Upper specimen: Right upper jaw with  $M^{3-5}$ , Y.P.M. No. 13748.  
Lower specimen: Right upper jaw with  $M^{1-4}$ , Y.P.M. No. 13749.  
Both crown views. X 6 diam.

FIG. 2. Right upper jaw with  $M^{3-5}$ , crown view. X 12 diam. Type. Y.P.M.  
No. 13738.

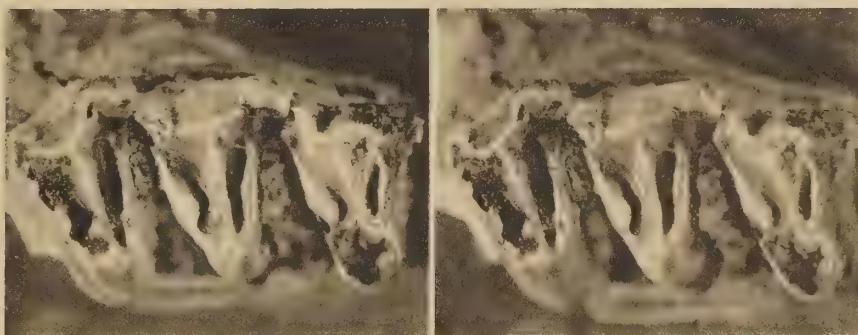
*Malthacolestes osborni* Simpson.

82

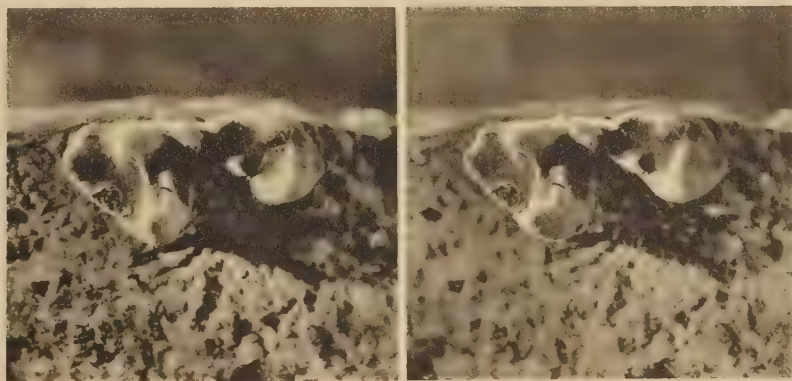
FIG. 3. Right upper jaw with  $M^{1-2}$ , crown view. X 15 diam. Type. Y.P.M.  
No. 13751.



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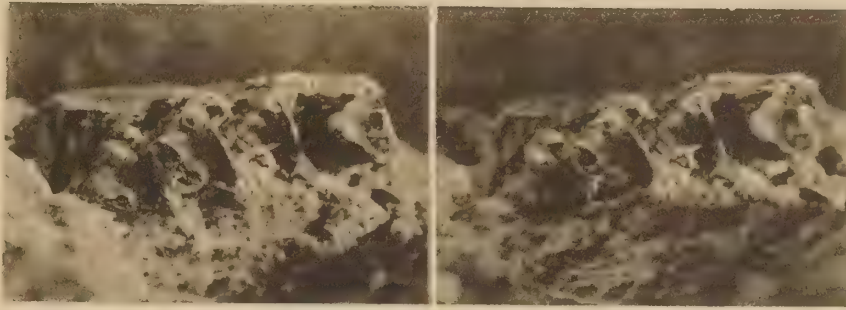


3

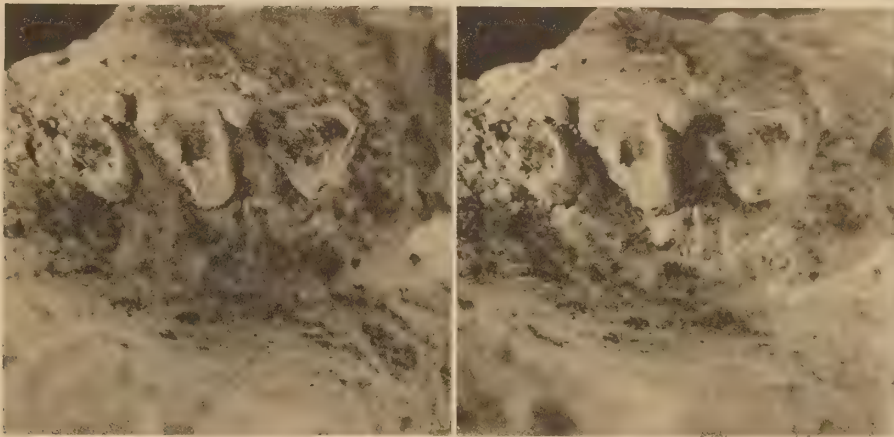


## PLATE XVI

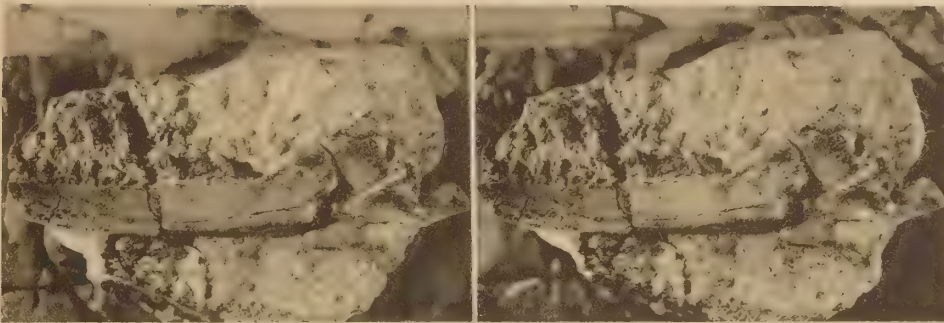
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|---|----------------------|
| <i>Euthlastus cordiformis</i> Simpson.  | 79                   |
| FIG. 1. Right upper jaw with last four molars, crown view. X 15 diam.<br>Type. Y.P.M. No. 13755.                              |                      |
| <i>Pelicopsis dubius</i> Simpson.   | 83                   |
| FIG. 2. Right upper jaw with last three molars, crown view. X 12 diam.<br>Type. Y.P.M. No. 13754.                             |                      |
| <i>Docodon striatus</i> Marsh.  | 93                   |
| FIG. 3. Right lower jaw with C, P <sub>1-4</sub> , and M <sub>1-5</sub> , internal view. X 2 diam.<br>Type. Y.P.M. No. 11823. |                      |



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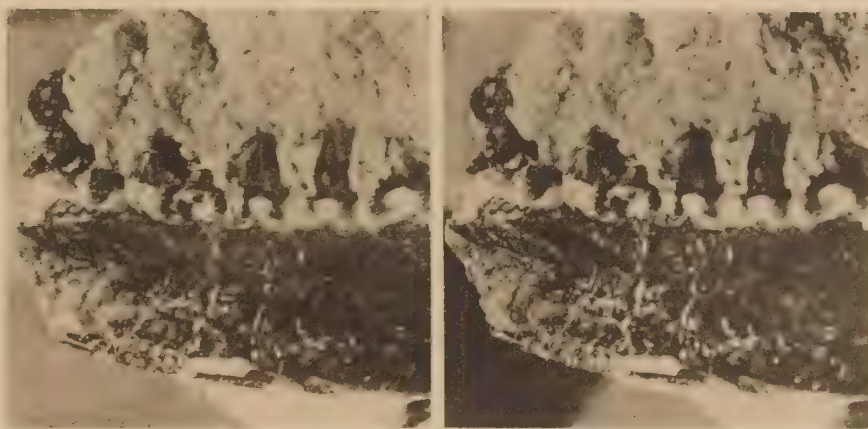


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## PLATE XVII

	Described on Page
<i>Docodon striatus</i> Marsh.	93
FIG. 1. Detail of same specimen as Pl. XVI, fig. 3, showing C, P <sub>1-4</sub> , and M <sub>1</sub> , internal view. X 8 diam. Type. Y.P.M. No. 11823.	
<i>Docodon victor</i> (Marsh).	90
FIG. 2. Detail of right lower jaw, showing C and P <sub>1-4</sub> , internal view. X 8 diam. Type. Y.P.M. No. 11826.	
FIG. 3. Same specimen, detail showing M <sub>4-6</sub> , internal view. X 10 diam.	

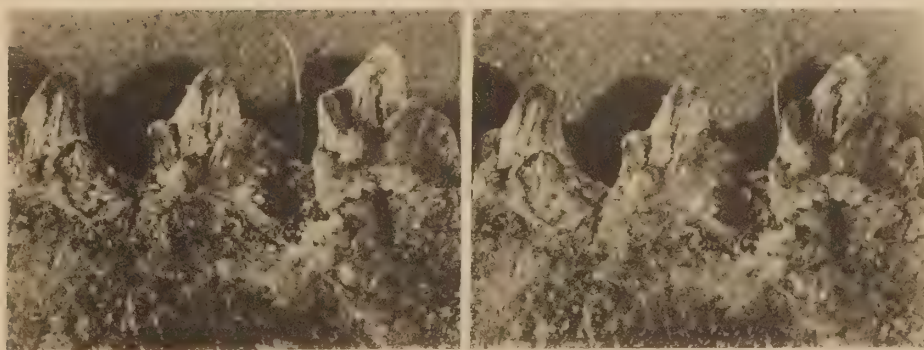




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## PLATE XVIII

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86

### *Docodon* sp.

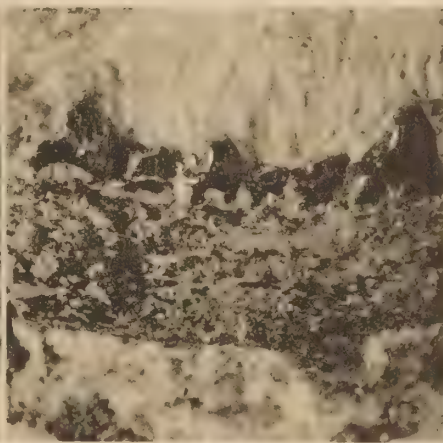
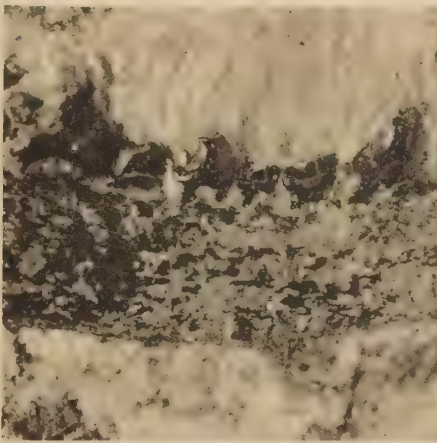
FIG. 1. Isolated right lower molar, crown view. X about 13 diam.

FIG. 2. Left lower jaw with C, P<sub>1-4</sub>, and M<sub>1</sub>, internal view. X about 6 diam. Y.P.M. No. 10649.

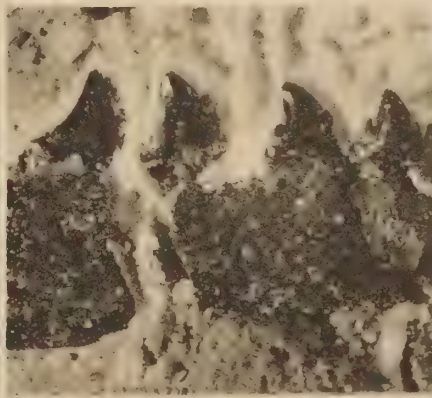
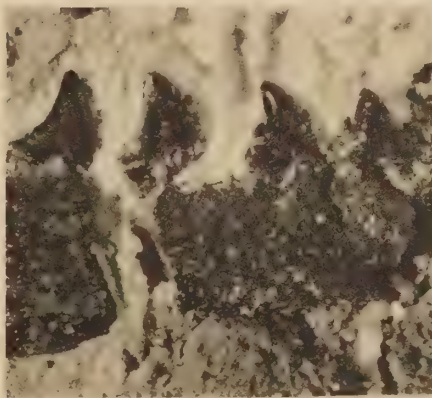
FIG. 3. Right lower jaw with P<sub>3-4</sub> and M<sub>1-2</sub>, external view. X about 6 diam. Y.P.M. No. 13734.



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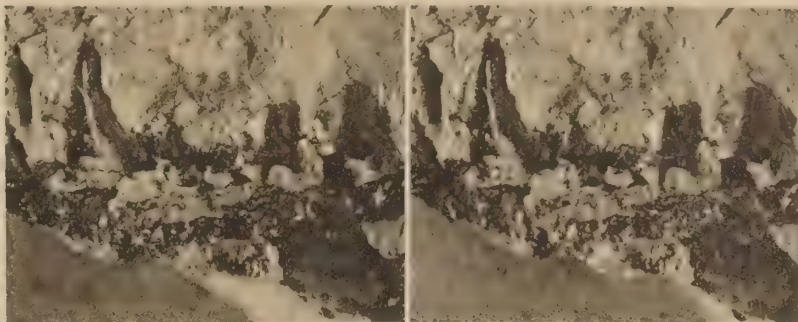


3

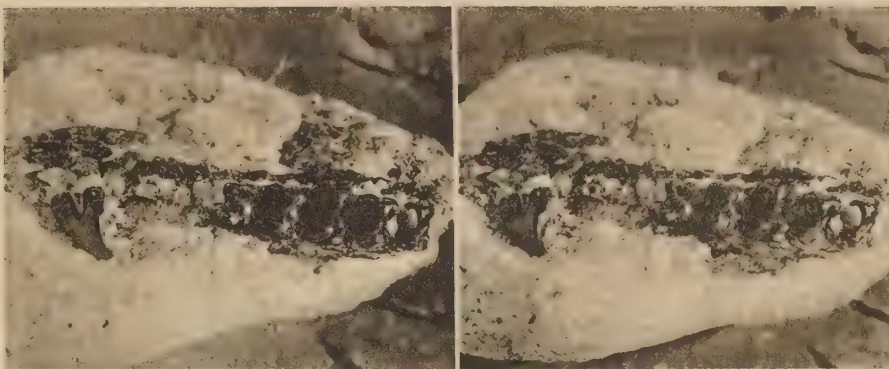


## PLATE XIX

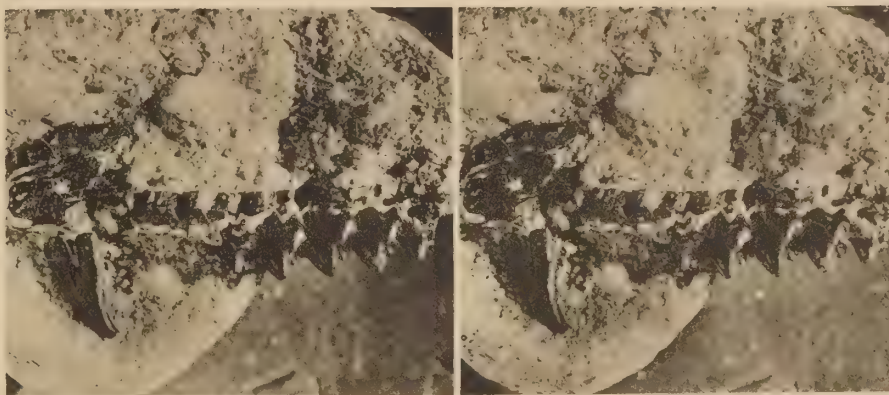
- |  | Described<br>on Page |
|--|----------------------|
| <i>Docodon</i> sp.   | 86                   |
| FIG. 1. Right lower C and P <sub>1-4</sub> , with impression of jaw, internal view.<br>X about 6 diam. Y.P.M. No. 13737. |                      |
| <i>Docodon superus</i> Simpson.  | 95                   |
| FIG. 2. Right upper jaw with C and M <sup>1-5</sup> , crown view. X 4 diam. Type.<br>Y.P.M. No. 10647.                   |                      |
| FIG. 3. Same specimen, internal view. X 4 diam.  |                      |



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## PLATE XX

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on Page

### *Docodon superus* Simpson.

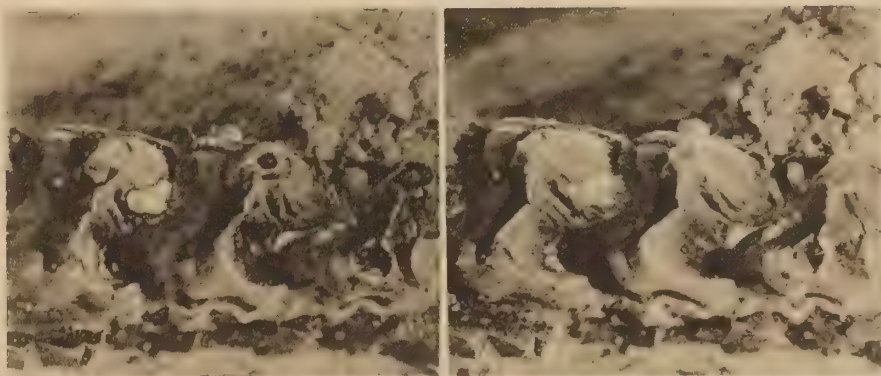
95

FIG. 1. Detail of same specimen as Pl. XIX, figs. 2-3, showing right  $M^{1-3}$ , crown view. X about 10 diam. Type. Y.P.M. No. 10647.

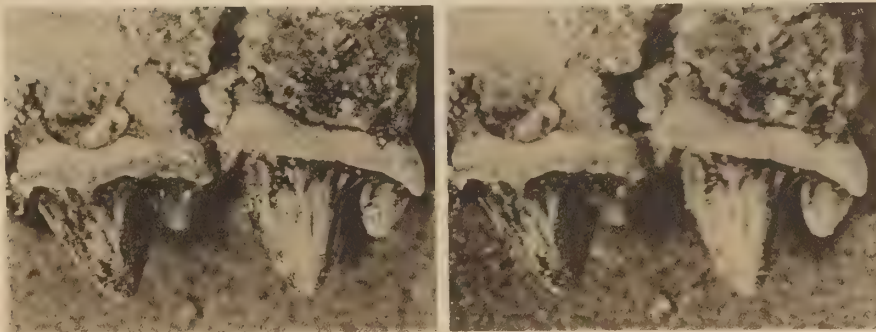
FIG. 2. Left  $M^{2-3}$ , external view. X about 12 diam. Y.P.M. No. 13770.

FIG. 3. Left upper jaw with C,  $P^{1-3}$ , and  $M^{1-2}$ , crushed and lying in matrix, somewhat oblique internal view. X about 6 diam. Y.P.M. No. 13769.

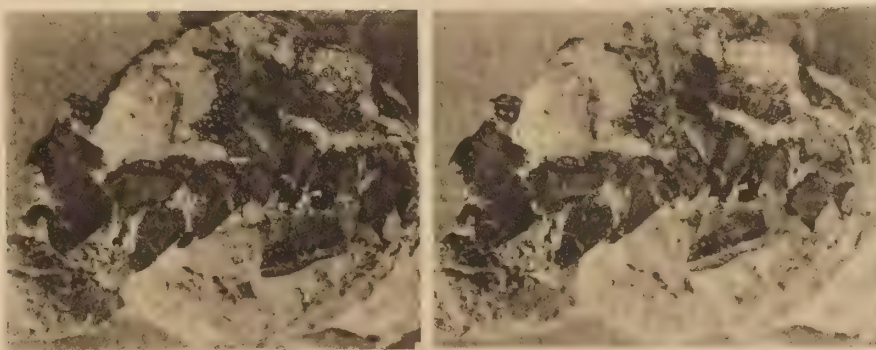




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PLATE XXI

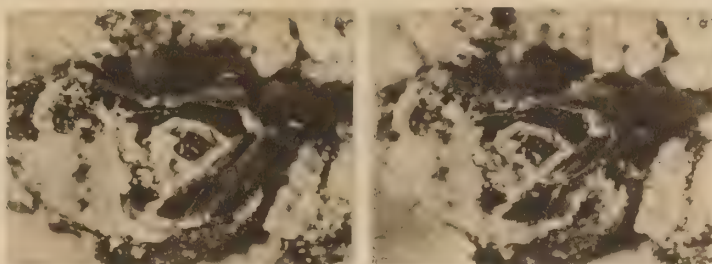
*Docodon superus* Simpson.

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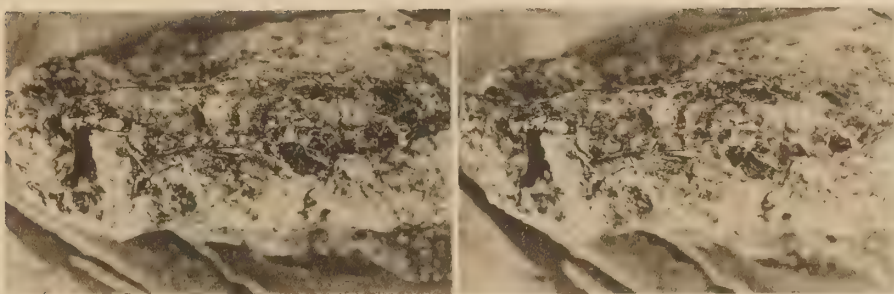
95

FIG. 1. Right P<sup>3</sup> in jaw, crown view. X about 15 diam. Y.P.M. No. 13770.

FIG. 2. Left upper jaw with fragments of teeth. X about 3 diam.



I



2



## PLATE XXII

Described  
on Page

### *Phascolodon gidleyi* Simpson.

31

FIG. 1. Fragment of left lower jaw with last two molars, external view. X 3 diam. Type. U.S.N.M. No. 2703. Photograph from the United States National Museum.

FIG. 2. Same, internal view. X 3 diam. Photograph from the United States National Museum.

### *Aploconodon comoënsis* Simpson.

32

FIG. 3. Fragment of right lower jaw with last two molars, internal view. X 3 diam. Type. U.S.N.M. No. 2791. Photograph from the United States National Museum.

### *Trioracodon bisulcus* (Marsh).

34

FIG. 4. Right lower jaw with parts of  $P_4$  and  $M_{1-3}$ , external view. X 5 diam. Type. Y.P.M. No. 11851.

FIG. 5. Same, crown view. X 5 diam.

FIG. 6. Left lower jaw with  $M_1$ , internal view. X 5 diam. Y.P.M. No. 10340.

FIG. 7. Right lower jaw with  $P_4$  and  $M_{1-2}$ , external view. X 5 diam. Y.P.M. No. 10345.

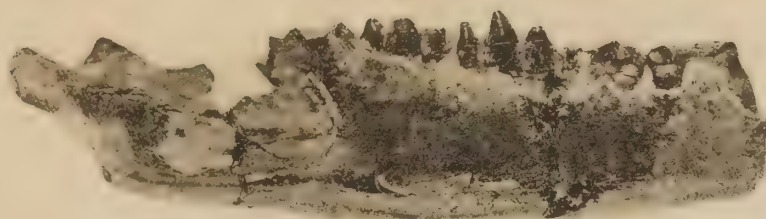
### *Priacodon robustus* (Marsh).

36

FIG. 8. Left lower jaw with  $P_{2-3}$ , and  $M_1$ , external view. X 5 diam. Y.P.M. No. 10343.

FIG. 9. Left lower jaw with  $P_3$  and  $M_{1-3}$ , internal view. X 5 diam. Type. Y.P.M. No. 11846.

FIG. 10. Same, external view. X 5 diam.



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1



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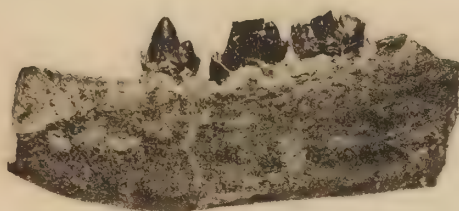
2



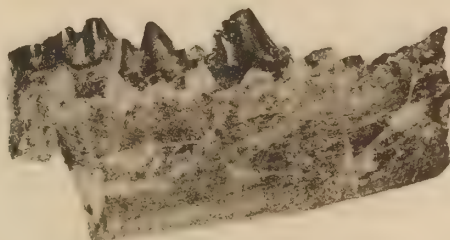
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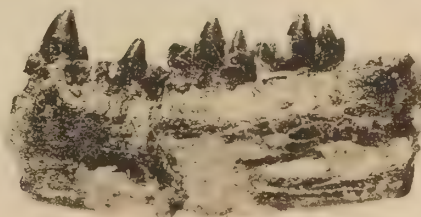
8



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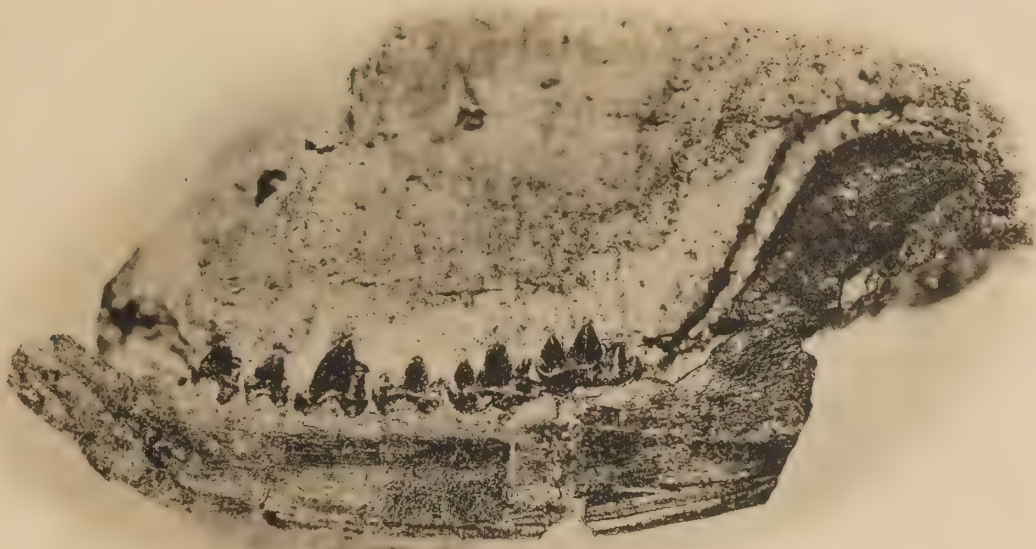
10

PLATE XXII—PHASCOLODON, APLOCONODON,  
TRIORACODON, PRIACODON

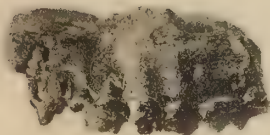
## PLATE XXIII

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|--|----------------------|
| <i>Priacodon ferox</i> (Marsh).  | 35                   |
| FIG. 1. Right lower jaw with P <sub>1-3</sub> and M <sub>1-3</sub> , internal view. X 5 diam.<br>Type. Y.P.M. No. 606.   |                      |
| <i>Trioracodon bisulcus</i> (Marsh).   | 34                   |
| FIG. 2. Left upper jaw with P <sup>3-4</sup> and M <sup>1-2</sup> , external view. X 4 diam.<br>U.S.N.M. No. 2699. Photograph from the United States National<br>Museum. |                      |
| FIG. 3. Same, internal view. X 4 diam. Photograph from the United<br>States National Museum.   |                      |
| FIG. 4. Left upper jaw with P <sup>4</sup> and M <sup>1-2</sup> , external view. X 6 diam.<br>Y.P.M. No. 10344.  |                      |

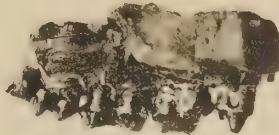




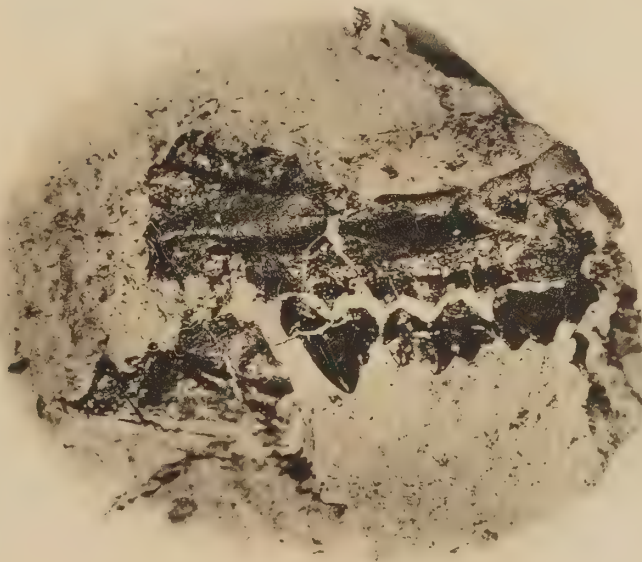
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## PLATE XXIV

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### *Priacodon ferox* (Marsh).

35

FIG. 1. Right upper jaw with  $M^{1-3}$ , external view. X 6 diam. Y.P.M. No. 13626.

FIG. 2. Same, more oblique view showing palate. X  $6\frac{1}{2}$  diam.

### *Priacodon grandaevus* Simpson.

37

FIG. 3. Left upper jaw with  $M^{1-3}$ , internal view. X 6 diam. Type. Y.P.M. No. 10349.

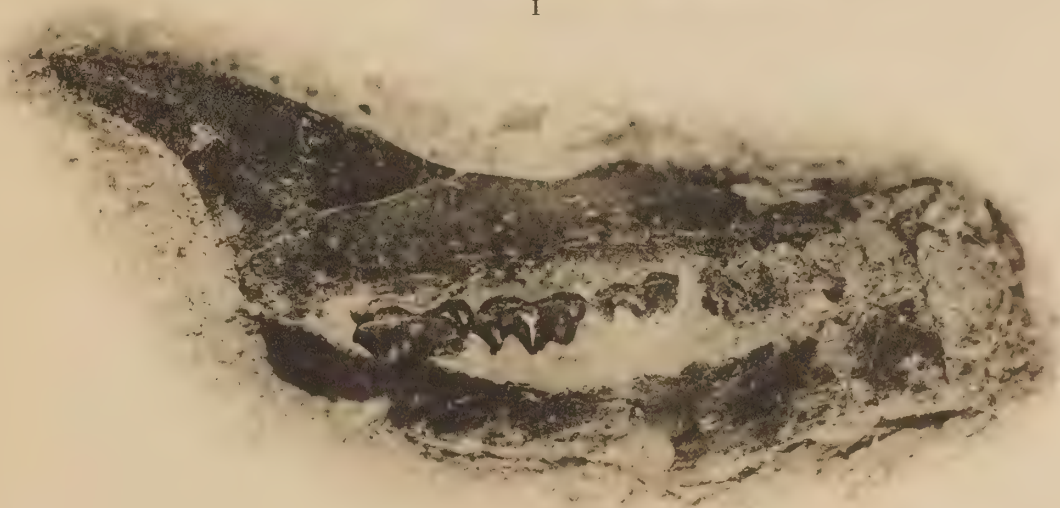
### *Priacodon lulli* Simpson.

36

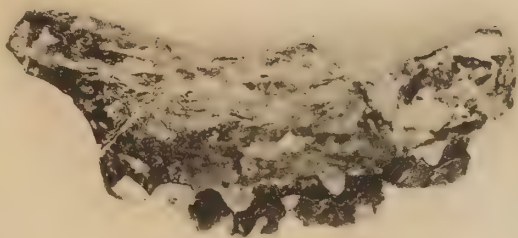
FIG. 4. Right upper jaw with  $P^3$  and  $M^{1-4}$ , internal view. X 6 diam. Type. Y.P.M. No. 13625.



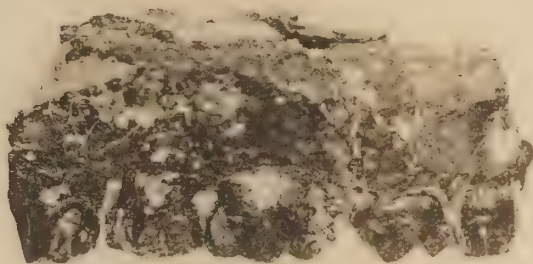
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## PLATE XXV

	Described on Page
<i>Priacodon lulli</i> Simpson.	36
FIG. 1. Right upper jaw with $M^{1-2}$ , external view. X 6 diam. Y.P.M. No. 10359.	
<i>Priacodon grandaevus</i> Simpson.	37
FIG. 2. Right upper jaw with $M^{1-3}$ , external view. X 5 diam. U.S.N.M. No. 2698. Photograph from the United States National Museum.	
<i>Amphidon superstes</i> Simpson.	41
FIG. 3. Right lower jaw with $P_4$ and $M_{1-4}$ , internal view. X 8 diam. Type. Y.P.M. No. 13638.	
FIG. 4. Same, detail showing $P_4$ and $M_{1-3}$ , internal view. X 12 diam.	
<i>Eurylambda aequicrurius</i> (Simpson).	42
FIG. 5. Right upper jaw with one molar, external view. X 7 diam. Type. Y.P.M. No. 13639.	

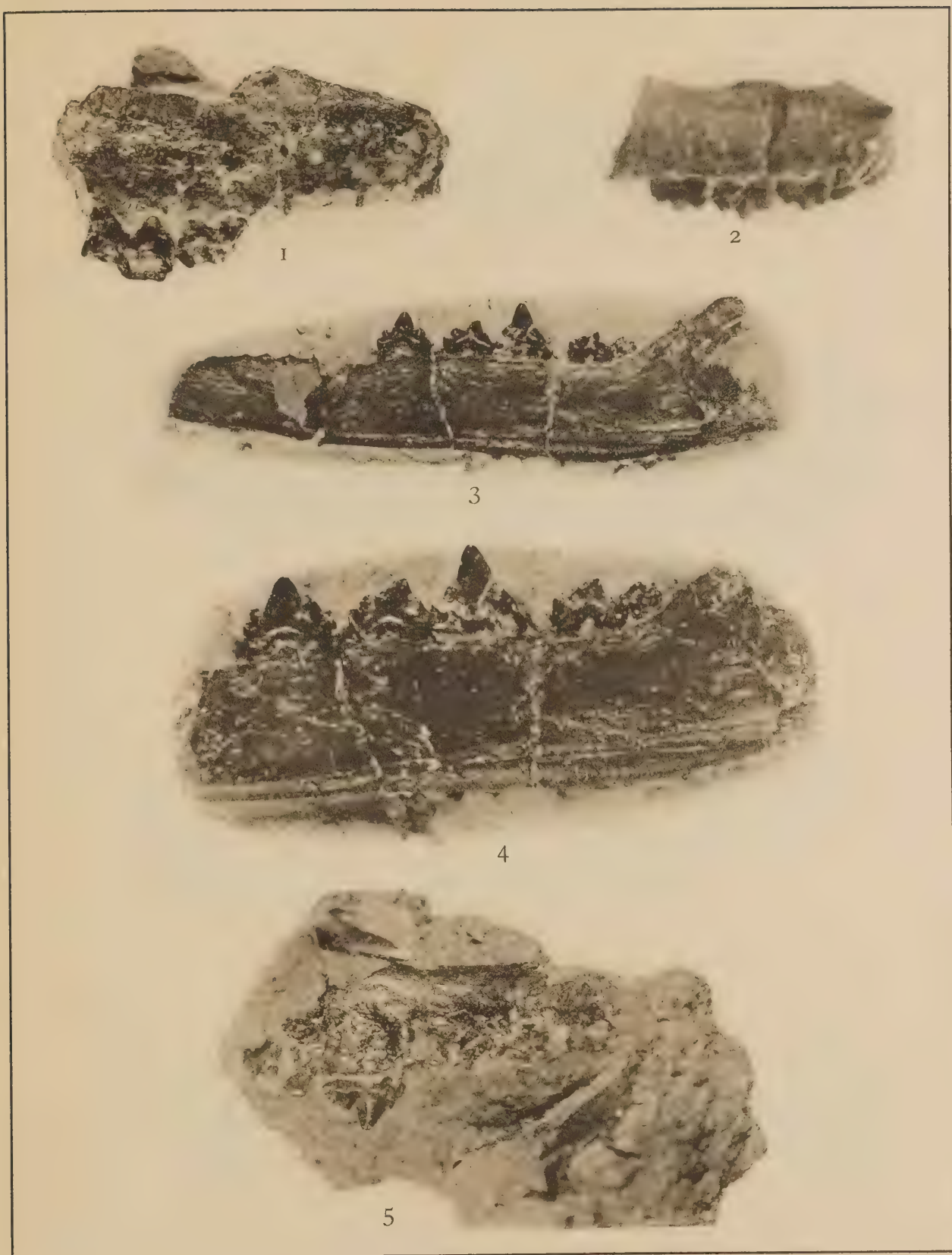


PLATE XXV—PRIACODON, AMPHIDON, EURYLAMBDA

## PLATE XXVI

- |   | Described<br>on Page |
|---|----------------------|
| <i>Eurylambda aequicrurius</i> (Simpson).   | 42                   |
| FIG. 1. Single upper molar, same specimen as Pl. XXV, fig. 5, posterior view. X 12 diam. Type. Y.P.M. No. 13639.  |                      |
| <i>Tinodon lepidus</i> Marsh.   | 39                   |
| FIG. 2. Left lower jaw with C, P <sub>1-3</sub> , and M <sub>1-3</sub> , internal view. X 3½ diam. (Type of <i>Menacodon rarus</i> .) U.S.N.M. No. 2131. Photograph from the United States National Museum. |                      |
| FIG. 3. Same, external view. X 3½ diam. Photograph from the United States National Museum.  |                      |
| FIG. 4. Left lower jaw with M <sub>1</sub> and M <sub>3</sub> , internal view. X 7 diam. Type. Y.P.M. No. 11845.  |                      |
| <i>Tinodon bellus</i> Marsh.  | 39                   |
| FIG. 5. Right lower jaw with M <sub>1-4</sub> , internal view. X 7 diam. Type. Y.P.M. No. 11843.  |                      |





PLATE XXVI—EURYLAMBDA, TINODON

## PLATE XXVII

- |   | Described<br>on Page |
|---|----------------------|
| <i>Ctenacodon scindens</i> Simpson.   | 20                   |
| FIG. 1. Left lower jaw with P <sub>2-4</sub> and M <sub>1</sub> , external view. X 10 diam. A.M.N.H. No. 28063. Photograph from the American Museum of Natural History.                               |                      |
| <i>Paurodon valens</i> Marsh.   | 49                   |
| FIG. 2. Left lower jaw with C, P <sub>1-2</sub> , and M <sub>1-4</sub> , external view. X 3 diam. Type. U.S.N.M. No. 2143. Photograph from the United States National Museum.                         |                      |
| <i>Archaeotrigon brevimaxillus</i> Simpson.   | 51                   |
| FIG. 4. Right lower jaw with C, P <sub>1-2</sub> , and M <sub>1-2</sub> , internal view. X 3 diam. Type. U.S.N.M. No. 2793. Photograph from the United States National Museum.                        |                      |
| FIG. 5. Same, crown view. X 3 diam. Photograph from the United States National Museum.  |                      |
| <i>Amblotherium gracilis</i> Marsh  | 66                   |
| FIG. 6. Left lower jaw with P <sub>4</sub> and M <sub>1-8</sub> , external view. X 3 diam. U.S. N.M. No. 2693. Photograph from the United States National Museum.                                     |                      |
| FIG. 7. Same, crown view. X 3 diam. Photograph from the United States National Museum.  |                      |
| FIG. 8. Left lower jaw with P <sub>3-4</sub> and M <sub>1-7</sub> , internal view, X 3 diam. (Type of <i>Laodon venustus</i> .) U.S.N.M. No. 2142. Photograph from the United States National Museum. |                      |

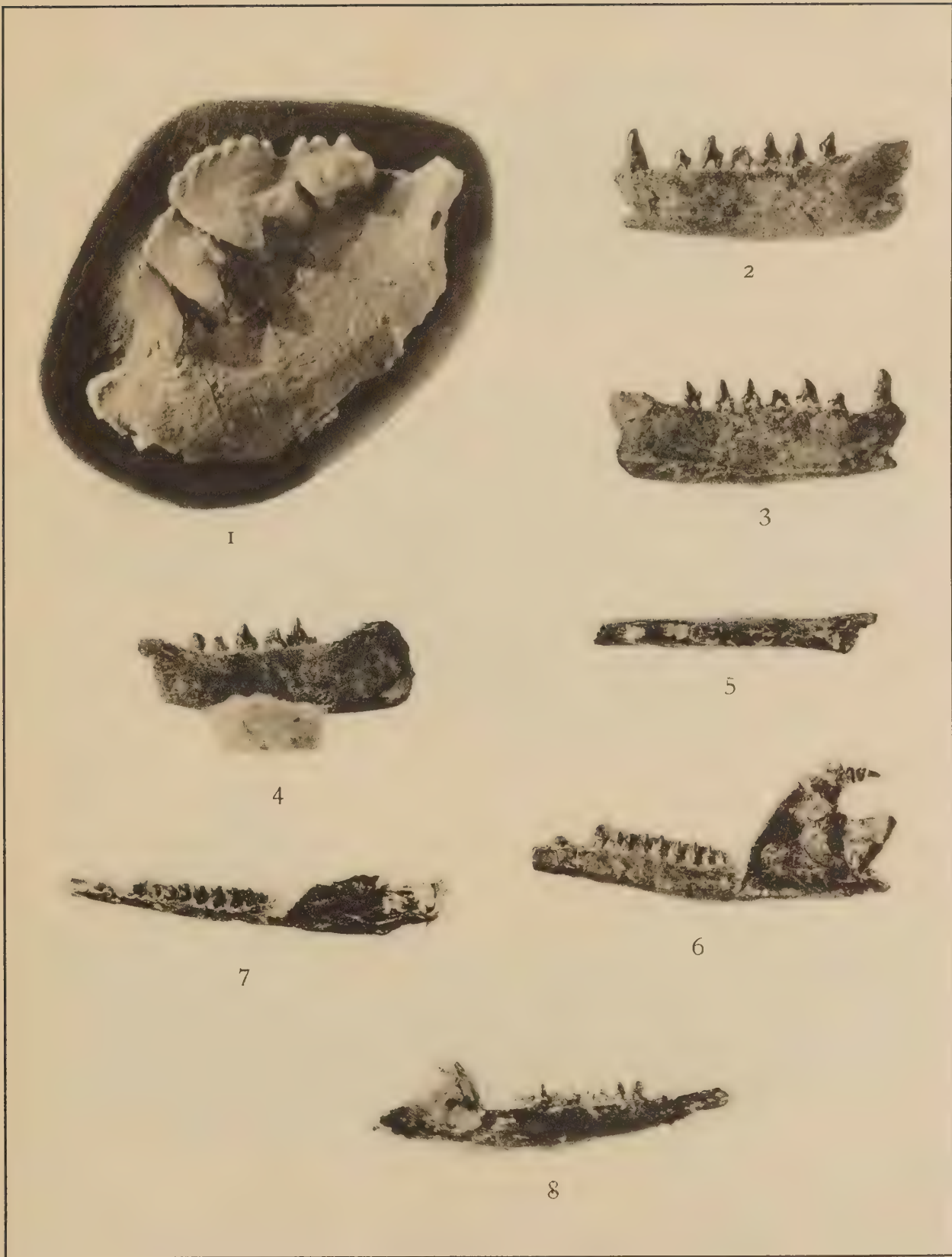


PLATE XXVII—CTENACODON, PAURODON,  
ARCHAEOTRIGON, AMBLOTHERIUM



## PLATE XXVIII

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on Page

### *Dryolestes priscus* Marsh.

58

FIG. 1. Right lower jaw with P<sub>3-4</sub> and M<sub>1-7</sub>, internal view. X 5 diam.  
Neotype. U.S.N.M. No. 2722. Photograph from the United States  
National Museum.

FIG. 2. Right lower jaw with P<sub>1-4</sub> and M<sub>1-7</sub>, external view. X 6 diam.  
(Type of *Asthenodon segnis*.) Y.P.M. No. 10646.

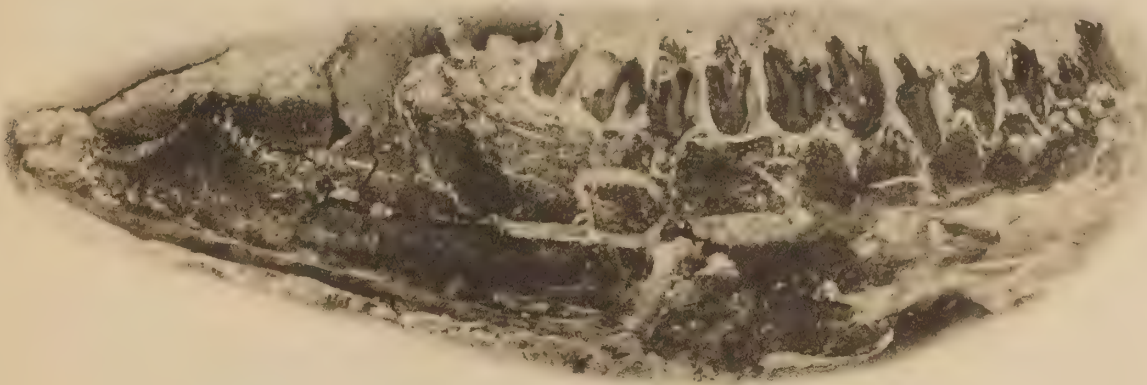
### *Laolestes eminens* Simpson.

61

FIG. 3. Left lower jaw with I<sub>3-4</sub>, C, P<sub>1-3</sub>, and M<sub>1-8</sub>, internal view. X 5  
diam. Type. Y.P.M. No. 13719.



1



2



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## PLATE XXIX

- |  | Described<br>on Page |
|--|----------------------|
| <i>?Laolestes</i> sp.  | 64                   |
| <p>FIG. 1. Anterior end of left lower jaw with I<sub>1-4</sub>, C, and P<sub>2</sub>, external view. X 5 diam. U.S.N.M. No. 2862. Photograph from the United States National Museum.</p>   |                      |
| <i>Laolestes eminens</i> Simpson.  | 61                   |
| <p>FIG. 2. Right lower jaw with four molars, internal view. X 5 diam. U.S. N.M. No. 2731. Photograph from the United States National Museum.</p> <p>FIG. 3. Left lower jaw with P<sub>3</sub>, M<sub>2</sub>, and M<sub>5-7</sub>, oblique external view. X 8 diam. A.M.N.H. No. 3001. Photograph from the American Museum of Natural History.</p> |                      |
| <i>Kepolestes coloradensis</i> Simpson.  | 70                   |
| <p>FIG. 4. Right lower jaw with P<sub>4</sub> and M<sub>1-8</sub>, internal view. X 5 diam. Type. U.S.N.M. No. 2723. Photograph from the United States National Museum.</p>  |                      |
| <i>Docodon striatus</i> Marsh.   | 93                   |
| <p>FIG. 5. Right lower jaw with C, P<sub>1-4</sub>, and M<sub>1-5</sub>, internal view. X 4 diam. Type. Y.P.M. No. 11823.</p>  |                      |





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PLATE XXIX—LAOLESTES, KEPOLESTES, DOCODON

## PLATE XXX

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### *Docodon victor* (Marsh).

90

FIG. 1. Right lower jaw with C, P<sub>1-4</sub>, and M<sub>1-6</sub>, internal view. X 4½ diam. Type. Y.P.M. No. 11826.

FIG. 2. Same, X-ray. Natural size.

FIG. 3. Left lower jaw with P<sub>3-4</sub> and M<sub>1-3</sub>, external view. X 5 diam. U.S. N.M. No. 2707. Photograph from the United States National Museum.

### *Docodon crassus* (Marsh).

94

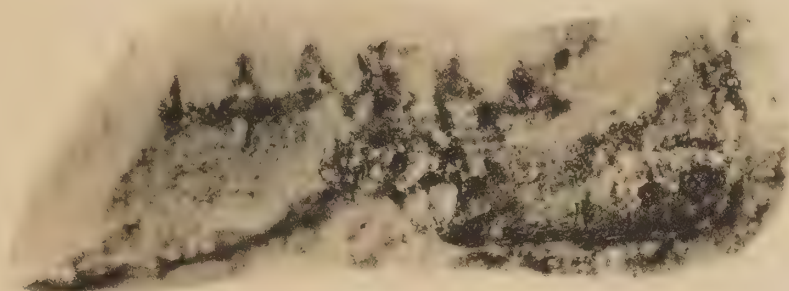
FIG. 4. Right lower jaw with C, P<sub>3-4</sub>, and M<sub>1-4</sub>, external view. X 4 diam. Type. U.S.N.M. No. 2130. Photograph from the United States National Museum.

### *Docodon* sp.

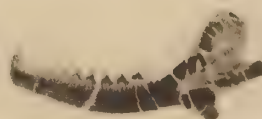
FIG. 5. Left lower jaw with six cheek teeth, external view. Specimen from Garden Park, Colorado. X 5 diam. U.S.N.M. No. 2717. Photograph from the United States National Museum.



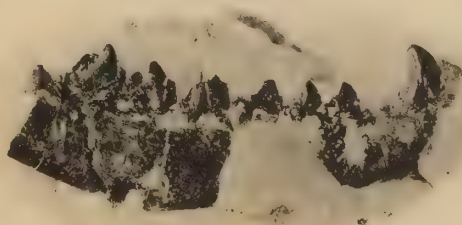
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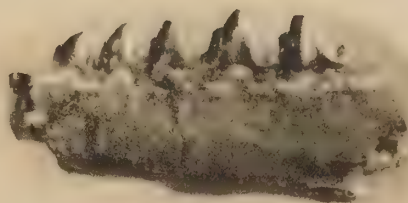
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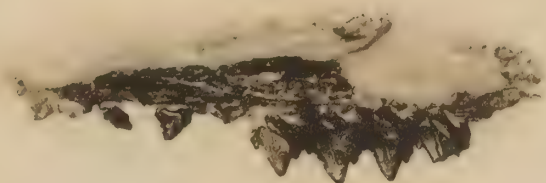


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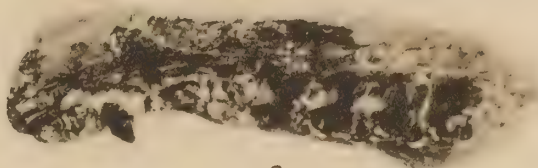


## PLATE XXXI

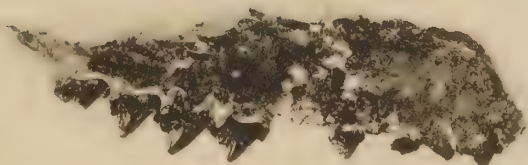
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<i>Docodon superus</i> Simpson.	95
FIG. 1. Right upper jaw with P <sup>1</sup> , P <sup>3</sup> , and M <sup>2-5</sup> , internal view. X 4 diam. U.S.N.M. No. 2715. Photograph from the United States National Museum.	
FIG. 2. Same, crown view. X 4 diam. Photograph from the United States National Museum.	
FIG. 3. Same, external view. X 4 diam. Photograph from the United States National Museum.	
<i>Meniscoëssus</i> sp.	104
FIG. 4. Isolated M <sub>1</sub> , crown view. X 8 diam.	
<i>Cimolomys</i> sp.	110
FIG. 5. Isolated M <sub>1</sub> , crown view. X 8 diam.	



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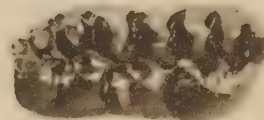
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## PLATE XXXII

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### *Nyssodon punctidens* Simpson.

120

FIG. 1. Isolated upper molar, crown view. X 13 diam. Type. Y.P.M. No. 13654.

FIG. 2. Same, posterior view. X 13 diam.

### *Gypsonictops hypoconus* Simpson.

138

FIG. 3. Isolated right M<sup>1</sup> or M<sup>2</sup>, posterior view. X 13 diam. Type. Y.P.M. No. 13662.

FIG. 4. Same, crown view. X 13 diam.

FIG. 5. Same, external view. X 13 diam.

FIG. 6. Isolated right P<sup>4</sup>, crown view. X 13 diam. Y.P.M. No. 13651.

FIG. 7. Isolated M<sup>3</sup>, crown view. X 13 diam.



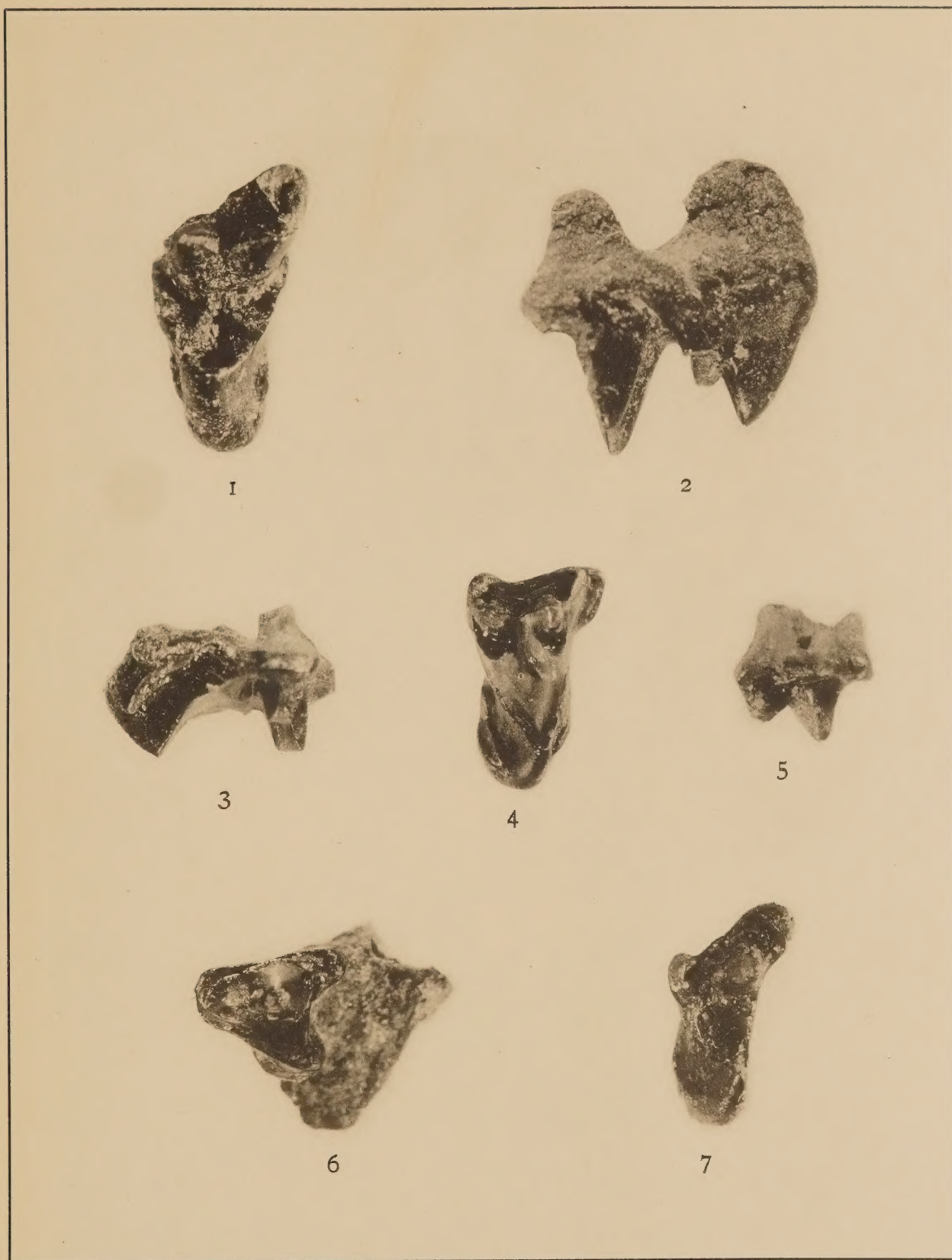


PLATE XXXII—NYSSODON, GYPSONICTOPS

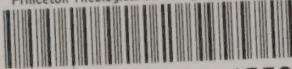






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